THE GENUS *CARAPICHEA* (RUBIACEAE, PSYCHOTRIEAE)[1]

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Abstract

The Neotropical species that have been included in *Psychotria* L. comprise a heterogeneous group, morphologically and systematically. *Carapichea* Aubl. (Rubiaceae, Psychotrieae) was separated from *Psychotria* based on molecular analyses to include *C. affinis* (Standl.) L. Andersson, *C. guianensis* Aubl., and *C. ipecacuanha* (Brot.) L. Andersson; two more species were later included based on morphological characters, *C. ligularis* (Rudge) Delprete and *C. lucida* J. G. Jardim & Zappi. Here *Carapichea* is reviewed morphologically and circumscribed to include 23 Neotropical species found from Nicaragua to southeastern Brazil that share characters of the stipules and inflorescence arrangement. The genus is diagnosed mainly by its distinctive stipules, while pyrene characters, previously considered characteristic for the genus, actually vary widely. A revised morphological description of the genus includes more variation than previously documented, which is outlined in the key to species. Seven informal species groups are separated and characterized, and the following new nomenclatural combinations are made here: *Carapichea adinantha* (Standl.) C. M. Taylor, based on *Retiniphyllum adinanthum* Standl. and the sole species of *Stachyococcus* Standl., which fully synonymizes *Stachyococcus* with *Carapichea*; *Carapichea altsonii* (Sandwith) C. M. Taylor, based on *Cephaelis altsonii* Sandwith; *Carapichea araguariensis* (Steyerm.) C. M. Taylor, based on *P. araguariensis* Steyerm.; *Carapichea crebrinervia* (Standl.) C. M. Taylor, based on *Cephaelis crebrinervia* Standl.; *Carapichea fimbriflora* (Steyerm.) C. M. Taylor, based on *P. fimbriflora* Steyerm.; *Carapichea franquevilleana* (Müll. Arg.) C. M. Taylor, based on *P. franquevilleana* Müll. Arg.; *Carapichea klugii* (Standl.) C. M. Taylor, based on *P. klugii* Standl.; *Carapichea maturacensis* (Steyerm.) C. M. Taylor, based on *P. maturacensis* Steyerm.; *Carapichea necopinata* (Standl.) C. M. Taylor, based on *P. necopinata* Standl.; *Carapichea nivea* (Sandwith) C. M. Taylor, based on *Cephaelis nivea* Sandwith; *Carapichea pacimonica* (Müll. Arg.) C. M. Taylor, based on *P. pacimonica* Müll. Arg.; *Carapichea panurensis* (Müll. Arg.) C. M. Taylor, based on *Mapouria panurensis* Müll. Arg.; *Carapichea sandwithiana* (Steyerm.) C. M. Taylor, based on *Cephaelis sandwithiana* Steyerm.; *Carapichea tillettii* (Steyerm.) C. M. Taylor, based on *P. tillettii* Steyerm.; *Carapichea urniformis* (Steyerm.) C. M. Taylor, based on *P. urniformis* Steyerm.; and *Carapichea vasivensis* (Müll. Arg.) C. M. Taylor, based on *Mapouria vasivensis* Müll. Arg. Newly described here is *Carapichea verrucosa* C. M. Taylor of Amazonian Peru, Colombia, and Brazil, which is notable for its relatively large, abaxially (i.e., dorsally) verrucose pyrenes.

Key words: Bolivia, Brazil, *Callicocca*, *Carapichea*, *Cephaelis*, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, IUCN Red List, Nicaragua, Panama, Peru, *Psychotria*, Psychotrieae, Rubiaceae, *Stachyococcus*, Surinam, *Uragoga*, Venezuela.

The Neotropical genus *Carapichea* Aubl. was described for a single species, *C. guianensis* Aubl., that was noted to be very similar to *Psychotria* L. (Rubiaceae, Psychotrieae; Aublet, 1775). *Carapichea* was originally separated from *Psychotria* based on inflorescence features, but was subsequently included by most authors in *Psychotria* or in the related genus *Cephaelis* Sw. Recent molecular systematic studies of *Psychotria* and related genera have significantly changed our understanding of relationships within the tribe Psychotrieae. These studies showed in particular that several morphological characters used to distinguish these genera are actually highly homoplasious (Nepokroeff et al., 1999; Andersson, 2002b). Based on these molecular data, the circumscription of *Psychotria* has been narrowed (Andersson, 2002b); the circumscription of *Palicourea* Aubl. has been expanded (Andersson, 2002b; Taylor & Gereau, 2010); and several genera have been separated from *Psychotria*. *Ronabea* Aubl. is now included in the tribe Lasiantheae (Taylor, 2004); *Coccochondra* Rauschert is included in Psychotrieae but its relationships are not clear (Taylor, 2011); and *Notopleura* (Benth. & Hook. f.) Bremek. (Taylor, 2001a), *Margaritopsis* Griseb. (Andersson, 2001; Taylor, 2005), and *Carapichea* (Andersson, 2002a) are included in Psychotrieae and apparently related to *Palicourea*.

Andersson (2002a, 2002b) separated *Carapichea* based on a broad molecular survey of world Psychotrieae and included in it three species that he studied with molecular data, *C. affinis* (Standl.) L. Andersson, *C. guianensis*, and *C. ipecacuanha* (Brot.) L. Andersson. Subsequently, two other species were

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added to *Carapichea* based on morphological characters: *C. ligularis* (Rudge) Delprete (Delprete, 2003) and *C. lucida* J. G. Jardim & Zappi (Jardim & Zappi, 2008). Here *Carapichea* is reviewed and its circumscription expanded to include 23 Neotropical species, based on morphological survey across the Neotropical species of Psychotrieae. Its taxonomy and morphology in this broadened circumscription are detailed as part of the ongoing study of the systematics of the Neotropical Psychotrieae (e.g., Taylor, 1996, 1997a, 2001a, 2005, 2011; Taylor & Gereau, 2010): the separation of *Carapichea* further clarifies the limits and characteristics of *Psychotria*, *Palicourea*, and related Neotropical genera.

Taxonomic History of *Carapichea*

The genus *Carapichea* was described by Aublet for one species from French Guiana, *C. guianensis* (Aublet, 1775), and Andersson (2002a) summarized its taxonomic treatment by subsequent authors. *Carapichea* was originally described as related to *Psychotria* and was distinguished from the latter genus by its combination of 5-merous flowers and terminal, capitate, pedunculate inflorescences enclosed by a pair of well-developed involucral bracts with acute apices. Generally taxonomists in the 19th and early 20th centuries included within *Psychotria* the species of Psychotrieae with small white flowers borne in branched inflorescences and separated the species with capitate inflorescences enclosed by well-developed involucral bracts variously in *Cephaelis*, *Uragoga* L. ex Baill., *Callicocca* Schreb., and/or *Carapichea*. In the same work, Aublet also described two other genera with capitate inflorescences enclosed by well-developed involucral bracts, *Tapogomea* Aubl. and *Evea* Aubl. *Tapogomea* included five species, all similar to *Carapichea*; *Tapogomea* apparently differed primarily in its inflorescences enclosed by external bracts with obtuse to truncate apices, in contrast to acute apices in *Carapichea*. *Tapogomea* is today considered a synonym of *Psychotria* subg. *Heteropsychotria* Steyerm. (Steyermark, 1972). *Evea* differed markedly from *Carapichea* in its 4-merous flowers and axillary inflorescence position (i.e., with inflorescences borne in both axils of the node). Aublet classified *Evea* together with *Coussarea* Aubl. and *Faramea* Aubl., based on its aristate stipules, 4-merous flowers, and fruits with a single thin-walled seed, which clearly distinguish it from *Psychotria* and related genera; *Coussarea* and *Faramea* are today included in a separate tribe from *Psychotria*, the Coussareeae (Bremer & Eriksson, 2009). *Evea* included only one species, *E. guianensis* Aubl., which clearly belongs to *Faramea* and is today treated as *F. guianensis* (Aubl.) Bremek. (Bremekamp, 1934; Boom & Delprete, 2002). However, some authors subsequently considered *Evea* to be closely related to *Psychotria* (e.g., de Candolle, 1830; Hooker, 1873; Schumann, 1891; Standley, 1916), which has generated some taxonomic confusion.

Swartz (1788) published the name *Cephaelis* for plants similar to *Psychotria*, but separated from the latter genus by their capitate inflorescences with well-developed involucral bracts. He included in *Cephaelis* four species from the Antilles and northern South America, two that were previously described and two that he described as new. The characters that distinguished *Cephaelis* were basically the same as those of *Carapichea* and *Tapogomea*, but Swartz did not explain its distinction from Aublet's genera even though he was familiar with them; one of the species he transferred to *Cephaelis* was *T. violacea* Aubl. In the following century and a half, the name *Cephaelis* was much more widely though incorrectly used than either of Aublet's older names, and subsequently the name *Cephaelis* was conserved with respect to *Carapichea*, *Tapogomea*, and *Evea* with its type conserved as *Cephaelis muscosa* (Jacq.) Sw. (McNeill et al., 2012).

Schreber (1789) published the name *Callicocca* for those species that Aublet (1775) had described variously in *Carapichea*, *Evea*, and *Tapogomea*; thus the name *Callicocca* is illegitimate because it was offered as an unnecessary substitute name when a previously published name should have been used. However, Schreber did not name any species in this genus or otherwise designate a type for *Callicocca*.

The genus name *Ipecacuanha* Arruda and its single species *I. officinalis* Arruda have been widely cited as synonyms of *Carapichea ipecacuanha* (e.g., Andersson, 2002a) and usually designated as illegitimate superfluous names. Arruda did not cite any previously published name, but clearly intended to name a new species. Unfortunately, he gave no descriptive information beyond the observation that this species is cultivated, and thus his names are nomina nuda. Rafinesque (1838) later independently published the name *Ipecacuanha* Raf., with one species, *I. fusca* Raf. Rafinesque noted that *I. fusca* included plants that had been called *Callicocca ipecacuanha* Brot., *Psychotria emetica* L. f. [= *Ronabea emetica* (L. f.) A. Rich.], and *Cephaelis emetica* (L. f.) Pers., but which Rafinesque considered a distinct species.

De Candolle (1830: 532–536) recognized *Cephaelis* and *Carapichea* as separate genera, and he synonymized *Callicocca* and *Evea* with *Cephaelis*. However, he commented that perhaps *Carapichea*

also should be included in *Cephaelis* and separated it only provisionally based on its "subexserted" anthers and stigmas together with its pyrenes that are smooth abaxially (i.e., dorsally) in contrast to the anthers included, the stigmas exserted, and the pyrenes ribbed abaxially in *Cephaelis*. The separation of these two genera by their anther and stigma position is problematic because many if not most species of both genera are distylous: each individual species includes both plants with long-styled (i.e., pin) flowers and plants with short-styled (i.e., thrum) flowers. However, distyly was not yet understood in 1830, and de Candolle separated the long-styled and short-styled flower forms of a single species taxonomically in some other cases as well (e.g., the long-styled and short-styled plants of *Psychotria bahiensis* DC. were included in separate varieties; de Candolle, 1830: 509). De Candolle's separation of *Carapichea* from *Cephaelis* was also problematic because the fruits of several of the species he included in both of these genera were unknown. De Candolle included two species in *Carapichea*: *Carapichea guianensis* with entire stipules, to which he gave the illegitimate new name *Carapichea aubletii* DC., and *Carapichea patrisii* DC. with bilobed stipules, which was subsequently synonymized with *P. hoffmannseggiana* (Willd. ex Roem. & Schult.) Müll. Arg. (Steyermark, 1972).

Contemporaneously Richard (1830: 174–175) in his review of the Rubiaceae differed from de Candolle in his classification of these genera. Richard synonymized both *Carapichea* and *Callicocca* under *Cephaelis*, even though *Carapichea* was the older name and thus had priority. He separated *Cephaelis* from *Psychotria* based only on inflorescence structure: compact and headlike or capitate in *Cephaelis* in contrast to openly or loosely branched in *Psychotria*.

Hooker (1873: 127) separated *Cephaelis* from *Psychotria* similarly to Richard, by its headlike or capitate inflorescences with well-developed involucral bracts, in contrast to openly or loosely branched inflorescences with small bracts in *Psychotria*. Hooker also synonymized several names similarly under *Cephaelis*, including *Carapichea*, *Evea*, and *Callicocca*, even though some of the synonymized names are older. He circumscribed *Psychotria* broadly otherwise, to include a number of species that today are classified variously in *Psychotria*, *Palicourea*, and other genera.

Baillon (1879a) intended to resurrect the name "Uragoga" as an overlooked Linnean name that should be used in place of several other generic names, but instead Baillon published *Uragoga* L. ex Baill. under his own authorship because Linnaeus (Linné, 1737) only used that name, spelled as "Ouragoga," in a work published before the 1753 starting date for botanical nomenclature (McNeill et al., 2012), so Linnaeus's name was not validly published. Therefore, *Uragoga* was not effectively published until 1879 and does not have nomenclatural priority over most of the genus names for this group. The publication of the name *Uragoga* is attributed to Baillon's overview article discussing it and circumscribing it (1879a), although this name was used by him in several binomials prior to that article (Baillon, 1879b). In his circumscription of *Uragoga*, Baillon synonymized 42 previously published generic names and thus rendered *Uragoga* an illegitimate superfluous name. Baillon circumscribed *Uragoga* very broadly, to comprise extensive morphological variation and a heterogenous group including most of the species of the Psychotrieae as well as some species now classified in other tribes. Baillon made few nomenclatural combinations in *Uragoga* for previously described species, but he did describe several new species in this genus. Petit (1964: 16) fixed the identity of *Uragoga* by selecting *U. ipecacuanha* (Brot.) Baill. as its lectotype.

Mueller (1881) studied the Psychotrieae of Brazil and some adjacent regions, and his classification differed substantially from that of previous authors (Taylor, 1996). Mueller separated Hooker's *Psychotria* into two genera, *Mapouria* Aubl., which generally corresponds to today's *Psychotria* subg. *Psychotria* (sometimes also called *Psychotria* s. str.), and "*Psychotria*," which generally corresponds to the Neotropical groups *Psychotria* subg. *Heteropsychotria* Steyerm. plus *Palicourea* (Steyermark, 1972) and to Andersson's *Palicourea* s.l. (Andersson, 2001). Mueller (1881: 163) separated *Mapouria* and *Psychotria* here based on pyrene form, in particular the presence or absence of an adaxial sulcus; however, in practice he certainly used some additional characters, because the fruits of a number of species that he classified were unknown to him. In contrast to previous taxonomists, Mueller regarded inflorescence features as widely variable within a genus, and accordingly he synonymized *Cephaelis*, *Palicourea*, and *Carapichea* and included their morphological variation all within his circumscription of *Psychotria*. (He did not study *Evea*, which was only known from outside his flora region.) The species included in *Carapichea* in its new circumscription here were classified by Mueller variously in *Mapouria* and *Psychotria*.

Schumann (1891: 119–120) followed Hooker in including species with branched inflorescences and small bracts in *Psychotria* and species with headlike or capitate inflorescences and well-developed bracts

in a separate genus. However, Schumann followed Baillon (1879a) and used the name *Uragoga* for this latter genus, though he circumscribed *Uragoga* more narrowly than Baillon did. Schumann also included several previously published names as synonyms of *Uragoga*, in particular *Cephaelis*, *Carapichea*, *Evea*, and *Callicocca*, and expanded the circumscription of *Cephaelis* to include some species with headlike inflorescences but without well-developed involucral bracts. Schumann followed Mueller (1881) in part as well and separated the species that were included in Hooker's *Psychotria* into two genera: *Mapouria*, which generally corresponds to today's *Psychotria* subg. *Psychotria*, and "*Psychotria*," which generally corresponds to *Psychotria* subg. *Heteropsychotria* minus the species with capitate inflorescences. Schumann did not present a species-level classification, but he accepted much of Mueller's classification, so the species included in the new circumscription here of *Carapichea* here were classified variously in Schumann's *Mapouria*, *Psychotria*, and *Uragoga*.

Kuntze (1891) followed Baillon's (1879a) taxonomy, recognizing a similarly broad circumscription of *Psychotria*, and used the name *Uragoga* for this group. He published hundreds of new nomenclatural combinations and replacement names for all the species of the genera that Baillon synonymized with *Uragoga*. Kuntze's classification was not adopted by subsequent authors.

In the 20th century Bremekamp studied Neotropical *Psychotria* and related genera in the Guianas, and noted that the species with headlike or capitate inflorescences and well-developed bracts that had been previously classified in *Cephaelis* comprised a heterogeneous group of species (Bremekamp, 1934: 297). Accordingly, he separated these species among several genera based on details of the arrangement and development of the inflorescence bracts: *Psychotria*, *Cephaelis*, *Petagomoa* Bremek., and *Gamotopea* Bremek. (the last two names are anagrams of *Tapogomea*, which Bremekamp cited as an older name for *Cephaelis*). Bremekamp included in *Cephaelis* only those species with flowers regularly subtended by bracts or bracteoles and rather broad, partially fused involucral bracts. He synonymized *Carapichea* here under *Cephaelis* and published the purportedly new nomenclatural combination *Cephaelis guianensis* (Aubl.) Bremek. for it; however, that combination had been previously published by Standley, making Bremekamp's name an isonym. Bremekamp synonymized two additional names with *Cephaelis guianensis*, *Cephaelis involucrata* Willd. and "*Cephaelis aubletii* DC." The name *Cephaelis involucrata* is an illegitimate name that was offered as an unnecessary substitute name for *Carapichea guianensis*; Bremekamp's name "*Cephaelis aubletii*" is apparently a typographical error for *Carapichea aubletii*.

In his various floristic surveys of Neotropical Rubiaceae, Standley (e.g., 1930, 1931a, 1931b, 1931c, 1936) separated *Cephaelis* from *Psychotria* based on details of the inflorescence features and development of the bracts. Standley did not study the plants of the Guianas in detail and did not explicitly cite *Carapichea* as a synonym of *Cephaelis* but did (Standley, 1929: 335) transfer the type species of *Carapichea* into *Cephaelis*, even though *Carapichea* is the older name. The name *Cephaelis* was conserved with respect to *Carapichea* in order to stabilize names in this group (e.g., Standley, 1916; Bremekamp, 1934); however, the name *Carapichea* is available when these genera are separated (Andersson, 2002a).

Steyermark (1972) extensively studied Neotropical *Psychotria* and related genera in northwestern South America, and presented a very different taxonomy from previous authors. Similarly to Mueller (1881) and to Petit studying *Psychotria* in Africa (1964), Steyermark regarded the branched versus headlike or capitate inflorescence structure as variable within a genus and did not separate *Cephaelis* from *Psychotria*. Similarly also to Mueller (1881), Steyermark divided the Neotropical species of *Psychotria* into two groups based on stipule morphology and pyrene morphology, which he treated as *Psychotria* subg. *Psychotria* and *Psychotria* subg. *Heteropsychotria*; however, he also separated *Palicourea*, which Mueller combined with the species of Steyermark's *Psychotria* subg. *Heteropsychotria*.[1]

[1] The differences between his two subgenera of *Psychotria* were presented in formal diagnoses (Steyermark, 1972: 444, 484), which distinguished them by stipule and pyrene features. In this work Steyermark also presented a key to individual species, in the course of which he keyed, or partially keyed, some of the infrageneric taxa. Several species from each subgenus are keyed in the first part of this, without mention of subgenera; then the remaining, less distinctive species are separated into subgenera in couplet #218 (of 405 couplets). Among these species the subgenera are separated by stipule features and drying color of the plants, and this has sometimes been considered Steyermark's functional separation of these two subgenera. These characters generally can be used to separate them in most cases. However, this lead keys less than half of the *Psychotria* species classified in this work, because the characters in couplet #218 do not key some of the species to subgenus, and Steyermark's formal diagnosis of the characters of *Psychotria* subg. *Heteropsychotria* does not include drying color. It may be that Steyermark intended couplet #218 of this key to diagnose the subgenera, and he did not in fact consider the pyrene characters meaningful (Kirkbride, pers. comm.), but that is not evident from internal evidence in this publication.

Steyermark synonymized several genera under *Psychotria* subg. *Heteropsychotria*, including *Cephaelis* (1972: 484), *Uragoga* (1972: 484), and *Carapichea* (1972: 676, this specifically listed under *Psychotria* sect. *Cephaelis* (Sw.) Müll. Arg.). As noted by Andersson (2002b) and Taylor (1996), Steyermark's *Psychotria* subg. *Psychotria* corresponded to pantropical *Psychotria* as circumscribed by Petit (1964), whereas the entirely Neotropical *Psychotria* subg. *Heteropsychotria* included the rest of the Neotropical species that were previously classified in *Psychotria* plus *Cephaelis* by Hooker (1873) and in *Psychotria* plus *Uragoga* by Schumann (1891). Steyermark's *Psychotria* subg. *Heteropsychotria* generally corresponds to Mueller's circumscription of *Psychotria* minus the species Steyermark separated in *Palicourea*. Thus, *Psychotria* subg. *Heteropsychotria* is morphologically very diverse (Taylor, 1996), and molecular studies have since shown that it comprises a systematically heterogeneous group of species (Andersson & Rova, 1999; Nepokroeff et al., 1999; Andersson, 2002b). As detailed in the individual discussions of the informal species groups presented here, the species that are included in the new circumscription of *Carapichea* here were variously classified by Steyermark in different sections and series of *Psychotria* subg. *Heteropsychotria*: *Psychotria* sect. *Cephaelis* (Sw.) Müll. Arg. (Steyermark, 1972: 676), *Psychotria* sect. *Notopleura* Oerst. ser. *Altsonii* Steyerm. (1972: 555), *Psychotria* sect. *Chytropsia* (Bremek.) Steyerm. (1972: 484), and the unnamed and undiagnosed *Psychotria* sect. 7 (1972: 574) and its unnamed and undiagnosed *Psychotria* ser. A (1972: 574) and *Psychotria* ser. C (1972: 588).

In his study of African *Psychotria*, Petit (1964) distinguished genera based primarily on pyrene and seed characters, in particular the presence and arrangement of preformed germination slits (PGSs) and the presence or absence of alcohol-soluble pigments in the seed coat. Pyrene morphology well characterizes *Psychotria* subg. *Psychotria* but is now known to be variable among the species included in *Psychotria* subg. *Heteropsychotria* (Piesschaert, 2001), and it is far from thoroughly reviewed or understood in this group. Some species and species groups are consistently characterized by pyrene morphology, but variation in pyrene characters within species groups and even within individual species has been documented as well (Piesschaert et al., 1998; Piesschaert, 2001). Steyermark discussed Petit's work and pyrene characters in his Neotropical *Psychotria* studies, but he did not document these extensively for the species he studied and did not really incorporate them into his classification. For example, several of the pyrene features that he said characterized some groups (e.g., *Psychotria* sect. *Chytropsia* (Bremek.) Steyerm.) are not actually found in all the species he included in those groups (Piesschaert, 2001). In practice, Steyermark's classification was based on other characters as well, apparently in particular stipule form, drying color of the specimens, and various details of the inflorescence arrangement.

Nepokroeff et al. (1999), Andersson and Rova (1999), and Andersson (2002a, 2002b) studied *Psychotria* and related genera using molecular sequence data and found two distinct clades, one including *Psychotria* subg. *Psychotria*. and the other comprising several genera including *Palicourea*, *Geophila* D. Don, *Chassalia* Comm. ex Poir., and *Rudgea* Salisb. This second clade has been variously called the *Palicourea* complex (Andersson, 2002a) or the *Palicourea* group (Andersson, 2001), and corresponds generally to the Palicoureeae of Robbrecht and Manen (2006) and Razafimandimbison et al. (2008). These studies also found that most of the Neotropical species included in *Psychotria* subg. *Heteropsychotria* are more closely related to *Palicourea* than to *Psychotria*. Andersson (2001) treated the species of *Psychotria* subg. *Heteropsychotria* plus *Palicourea* as a combined group he called *Palicourea* s.l.; however, he excluded several species from *Psychotria* subg. *Heteropsychotria* that were placed on a sister clade to *Palicourea* s.l. in the molecular analyses. *Palicourea* s.l. includes at least 600 species that currently have names variously in *Palicourea* and *Psychotria* and in many cases are very poorly known, and it has no comprehensive infrageneric classification; these genera are currently being combined and an infrageneric classification outlined bit by bit as the species are studied (e.g., Taylor et al., 2010).

In their molecular analysis, Nepokroeff et al. (1999) studied one species now included in *Carapichea*, *Psychotria ipecacuanha* (Brot.) Stokes (= *Carapichea ipecacuanha*), and found this species to be placed in the large clade that included *Palicourea* together with *Geophila* and *Chassalia*, but in a separate subclade from *Palicourea*. They called this subclade Other Psychotrieae. Andersson (2001) studied a different species that is now included in *Carapichea*, *Psychotria ligularis* (Rudge) Steyerm., and found that species included in his *Palicourea* group. The identity of the plant Andersson studied as *Psychotria ligularis* was subsequently clarified: the specimen identified as *Psychotria ligularis* in those studies (e.g., Andersson, 2001, 2002b) is the same collection, *Andersson et al. 1989* (MO!), that was later

re-identified as *Carapichea guianensis* (Andersson, 2002a: 364). As clarified by Delprete (2001, 2003), *C. guianensis* and *C. ligularis* are two different species, and this particular voucher specimen belongs to *C. guianensis*. (These two species were synonymized by Steyermark [1972] so the identifications used by Andersson all followed current taxonomy of the time.)

Andersson (2002a) used these results to focus on the relationships of several species of the *Palicourea* group in more detail and found *Psychotria ipecacuanha* (= *Carapichea ipecacuanha*) placed in a well-supported clade together with *Psychotria borucana* (Ant. Molina) C. M. Taylor & W. C. Burger (= *C. affinis*) and *Psychotria guianensis* (= *C. guianensis*). Accordingly, he placed these three species into a separate genus, for which he revived the name *Carapichea* based on the inclusion of its type species, *C. guianensis*. Andersson presented a morphological characterization and diagnosis of *Carapichea* but left the full species circumscription and further morphological detailing of this genus for the future. Instead of presenting a complete diagnosis of *Carapichea*, he outlined the morphological characters that separate it by distinguishing the related genera. He distinguished *Chassalia*, *Geophila*, *Margaritopsis*, *Notopleura*, and *Rudgea* from *Carapichea* by their different arrangements of the PGSs of the pyrenes and separated *Hymenocoleus* Robbr. from *Carapichea* by its ochrea-like structures on the stem nodes inside the stipules, which are lacking in *Carapichea* (Andersson, 2002a: 370) and in fact unique in the Rubiaceae. He also separated *Carapichea* from *Psychotria* subg. *Psychotria* by its "non-caducous stipules, pyrenes with distinct germination slits on abaxial ridges (rather than marginally) and testa without ethanol-soluble pigment," and a lack of ant domatia (2002a: 370) in contrast to caducous stipules, pyrenes with marginal PGSs, and seed testa with an ethanol-soluble red-brown pigment, along with the ant domatia found in a very few species of *Psychotria*. However, the characters that he cited to separate *Carapichea* from *Psychotria* are all found in *Palicourea*, so Andersson (2002a: 370) then separated these last two genera: "*Carapichea* differs from *Palicourea* s. l. in having aperturate pollen, and furthermore . . . in not having bipartite stipule lobes and in having the adaxial pyrene furrow with irregular (rather than smooth) margins, in contrast to inaperturate pollen, bipartite stipules, and pyrenes with an adaxial furrow with entire or smooth margins in *Palicourea*."

Delprete (2001) studied *Psychotria ligularis* as circumscribed by Steyermark (1972) and concluded that it comprised two distinct species, *P. ligularis* and *P. carapichea* (Steyerm.) Delprete. Shortly afterward Delprete followed Andersson in recognizing *Carapichea* (Boom & Delprete, 2002; Delprete, 2003), clarified that *P. carapichea* is correctly called *C. guianensis* (Delprete, 2003), and added a fourth species to the genus, *C. ligularis* (Delprete, 2003).

Jardim and Zappi (2008) subsequently described an additional species, *Carapichea lucida* J. G. Jardim & Zappi from eastern Brazil, and rather significantly emended Andersson's morphological characterization of this genus. They stated that *C. lucida* "is well placed within the genus *Carapichea* based on its marcescent stipules, its fruit colour, which is purple and dyes alcohol with a deep purple tinge, the presence of one basal-ventral pregermination slit [i.e., the pyrene with one basal-adaxial PGS], and its glomerulate inflorescence protected by green bracts." The marcescent stipules they cited agree with the general morphological characterization of *Carapichea* by Andersson (2002a), although this character was not noted by him to diagnose the genus and also characterizes some other genera of Psychotrieae (e.g., *Margaritopsis*; Taylor, 2005). Their characterization of *Carapichea* as having a "basal-ventral" germinal slit on the adaxial face of pyrene differs markedly from Andersson's description of PGSs located along the ribs of the abaxial surface of the pyrene. Fruit color and fruit pigments were not cited as diagnostic for *Carapichea* by any previous authors; Andersson (2002a: 371) characterized the genus as having variously "orange, red, blue, purplish, or blackish" fruits. Andersson also characterized the inflorescences of *Carapichea* as "congested and involucrate" (2002a: 371), but he did not mention the bract color nor did he include the inflorescence arrangement in a list of diagnostic features.

In a broad analysis of available molecular systematic data in Rubiaceae, Robbrecht and Manen (2006) also found *Carapichea* to be much more closely related to *Palicourea* than to *Psychotria*, and they included it in their newly described tribe Palicoureeae. In a study of the Psychotrieae and closely related tribes, Razafimandimbison et al. (2008) also found the Palicoureeae well supported by molecular data; however, their analysis did not include *Carapichea*. In a broad molecular analysis of all of Rubiaceae with more taxon sampling than previous works (Bremer & Eriksson, 2009), the species of *Carapichea* that were studied (*C. ipecacuanha* and *C. affinis*, identified there as *Psychotria ipecacuanha* and *P. borucana*) were placed on a large clade that included *Palicourea* and several other genera and within this on a separate subclade from *Palicourea* together with *Geophila* plus one species of

Chassalia (*C. parviflora* Benth.); the other species of *Chassalia* were placed on a different clade. Bremer and Eriksson did not separate Palicoureeae from Psychotrieae here, noting that their classification was conservative, and they found the support here for two tribes very weak.

Characterization and Circumscription of *Carapichea*

Andersson (2002a) presented a morphological characterization of *Carapichea* based on both the characters it possesses and the characters that are found in other genera but lacking in *Carapichea* based on study of three species that were incompletely known. Andersson separated *Carapichea* based on, overall, the presence of PGSs located along the abaxial ridges of the pyrenes, "non-caducous stipules," aperturate pollen, and adaxial pyrene furrows with irregular margins, along with the lack of ochrea-like structures on the stem nodes, ethanol-soluble pigments in the testa, and bipartite stipule lobes. Jardim and Zappi (2008) later considered *Carapichea* to be additionally diagnosed by the presence of marcescent stipules, glomerulate inflorescences enclosed by green involucral bracts, purple fruit with an alcohol-soluble purple pigment, and pyrenes with a single basal-adaxial PGS. The stipule form, fruit color, and inflorescence characters cited by Jardim and Zappi do not conflict with the species included in *Carapichea* by Andersson, except the inflorescence bracts of *C. affinis* are often purple rather than green. However, the form of the pyrene PGSs they describe does conflict with that noted by Andersson, which shows that either *C. lucida* is incorrectly classified or Andersson's morphological characterization of *Carapichea* merits some review now that more specimens are available. Accordingly several of Andersson's characters, the pollen, stipules, and pyrenes, are re-evaluated here; the ochrea-like stem structures and ethanol-soluble pyrene pigments are absent from *Carapichea* as circumscribed here.

Andersson (2002a) studied the pollen of two *Carapichea* species, *C. affinis* and *C. ipecacuanha*, but did not have flowers of *C. guianensis* available. He found the pollen to be aperturate and noted that in contrast the species of *Palicourea* s.l. studied all have inaperturate pollen. Andersson's characterization of the pollen of *Palicourea* cited Johansson's (1992) study of 12 species that molecular analyses showed belong to *Palicourea* s.l. Additionally, based on morphological characterization (Taylor, 1996), nearly all of the ca. 50 species that were included in Johansson's Neotropical group XXI and group XXII, both with inaperturate pollen, belong to *Palicourea* s.l.; however, an exception here is *Psychotria patria* Standl. & Steyerm. of group XXI, which is now included in *Notopleura patria* (Standl. & Steyerm.) C. M. Taylor (Taylor, 2001a). Andersson (2002a: 36) himself noted in his characterization of *Carapichea* that inaperturate pollen is a "homoplasious synapomorphy" found in some individual species belonging to various genera of Psychotrieae that generally have aperturate pollen (e.g., *Rudgea*, *Hymenocoleus*, *Chassalia*). Thus, aperturate pollen does characterize *Carapichea*, but future discovery of inaperturate pollen in the genus is not precluded.

"Bipartite stipule lobes" (Andersson, 2002a: 370), also called bifid stipules (Andersson, 2002a: 369) or bilobed stipules (Taylor, 1996), is the most common stipule form in Psychotrieae. This has been cited as characteristic of several genera, but both interpetiolarly entire and interpetiolarly bifid stipules are found in many Psychotrieae genera (e.g., *Notopleura*, *Margaritopsis*, *Chassalia*). Thus, variation may be expected in stipule form within *Carapichea* as well, and in fact the three species included in *Carapichea* by Andersson vary widely in this: *C. ipecacuanha* has multi-lobed or fimbriate stipules; *C. affinis* has ovate entire stipules; and *C. guianensis* has stipules that range from entire to minutely bilobed, entire then tardily splitting into two segments, or initially bilobed for up to half their length (e.g., *Feuillet & André 1405*, MO!). This variation in stipule form in *C. guianensis* has not been noted in the very few published descriptions of this species (e.g., Boom & Delprete, 2002), but is apparent when specimens are studied in detail. Thus, the stipule form cited by Andersson does not diagnose *Carapichea*.

As noted by Petit (1964) and Piesschaert (2001), some pyrene characters are diagnostic for some genera of Psychotrieae, in particular the presence and arrangement of PGSs and the presence of ethanol-soluble pigments in the testa. Andersson (2002a) studied pyrene morphology of *Carapichea guianensis* and *C. affinis*, but did not have fruits available of *C. ipecacuanha*. The pyrenes of the two species he studied lack ethanol-soluble pigments and have the PGSs located along the abaxial ridges. Andersson characterized *Carapichea* by the arrangement of the PGSs and the form of the adaxial pyrene furrow or groove, in particular by its well-developed irregular margins. These pyrenes are similar in the PGS arrangement and the deep adaxial furrow to species of *Palicourea* s.l., where Piesschaert (2001: 309) found apparently similar furrow margins in several species (e.g., *Palicourea pittieri* Standl., *Psychotria capitata* Ruiz & Pav.) and some other genera (e.g., *Chassalia*, Piesschaert et al., 2001). He also documented

variation in the furrow margins from rudimentary to well developed, even within some individual species such as *C. ligularis* (Piesschaert, 2001: 280, as *Psychotria ligularis*). In addition, none of Andersson's characteristic features of *Carapichea* are found in the pyrenes of *C. ipecacuanha*, for which fruits are now available. These pyrenes have a weak line or ridge instead of a furrow on the adaxial surface (Fig. 1A–C) and dehisce along the adaxial face through a basal pore and a short medial slit. Thus, the arrangement of their PGSs is similar to that of *C. lucida*. The pyrenes of *C. ipecacuanha* are also longitudinally twisted, a form previously known only in *Geophila* (Piesschaert et al., 1998). Thus, the pyrene characters cited by Andersson do not completely separate *Carapichea* from other genera, and the PGS arrangement of *C. lucida* is not unique in the genus.

The species that have been included in *Carapichea* do share several other distinctive morphological features that apparently diagnose this genus and identify additional species for inclusion in *Carapichea*. The characters that are here considered together to diagnose *Carapichea* are: a characteristic marcescent stipule form, inflorescences that are capitate or branched to one to two orders with the flowers sessile to shortly pedicellate, lack of ethanol-soluble pigments in the testa, and aperturate pollen of a generalized form. Based on these characters, 18 additional species are here transferred to *Carapichea*, which expands the morphological features found in this genus as discussed in more detail in the next section. In particular, there is rather extensive variation in stipule shape, inflorescence form, and the arrangement of the preformed germination slits of the pyrenes. Although *C. lucida* is quite distinctive, it agrees with the morphological characters found in this genus and appears to be correctly classified. Additionally, recent phytochemical analyses indicate that *Carapichea* also differs markedly in the chemistry of its alkaloids from *Psychotria* subg. *Heteropsychotria* and *Psychotria* subg. *Psychotria* (Bernhard et al., 2011), but taxonomic sampling in those analyses is still very limited. All the molecular studies of the tribe Psychotrieae have found very complex systematic patterns that are not yet well understood, both in the tribe and within the species-rich genera, so the expanded delimitation and morphological characterization of *Carapichea* presented here provide a detailed hypothesis that can now be tested further.

The relationships of *Stachyococcus* Standl. within the tribe Psychotrieae have been unclear (Taylor, 1996), but it has the characters of *Carapichea* as circumscribed here, in particular the stipule features, its flowers sessile in headlike glomerules borne in unbranched inflorescences, its relatively large fruits for *Palicourea* s.l., and the general similarity of its leaf venation to some other species of *Carapichea*, such as *C. klugii* (Standl.) C. M. Taylor. Accordingly, this species is here included in *Carapichea*.

The relationships of the species of *Psychotria* ser. *Altsonii* have also been unclear. Steyermark (1972: 555) grouped these four poorly known species together based on the arrangement of the inflorescence bracts and the supposedly sheathing truncate stipules and considered them related to *Notopleura*. Taylor et al. (2004) also considered these species related to *Notopleura* based on their habit, stipule form, leaf characters, and inflorescence arrangement. However, more detailed study shows that these all differ from *Notopleura* in their consistently terminal inflorescences and interpetiolar rather than sheathing stipules that lack glandular appendages. These four species are provisionally grouped together here based on Steyermark's observations and are included in *Carapichea* based on their inflorescence arrangement and stipules. Their stipules are interpetiolar and become marcescent with age, then fall off through fragmentation, leaving a markedly thickened scar (*C. altsonii* (Sandwith) C. M. Taylor) or hardened persistent basal portion (the three other species).

The species of *Carapichea* are arranged here in informal groups, which are partly characterized by one or a few morphological features. The separation of these groups aids identification of the species and highlights the morphological variation in this genus. The features that characterize these species groups may also indicate relationships, but many of the species are very poorly known. *Carapichea* itself is not well understood; these groups are therefore provisional and not formally named here.

Morphological Survey of the Species of *Carapichea*

A number of morphological features vary within *Carapichea*, including details of the stipule shape, degree of inflorescence branching, arrangement and development of the inflorescence bracts, corolla size and color, pollen form, fruit size and color and form and dehiscence mode of the pyrenes. However, these same features also vary within related genera (e.g., *Notopleura*, Taylor, 2001a; *Palicourea*, Taylor, 1997a), so this variation is not necessarily exceptional within *Carapichea*.

VEGETATIVE MORPHOLOGY

The dried specimens of many *Carapichea* species share a distinctive grayish green, grayish brown,

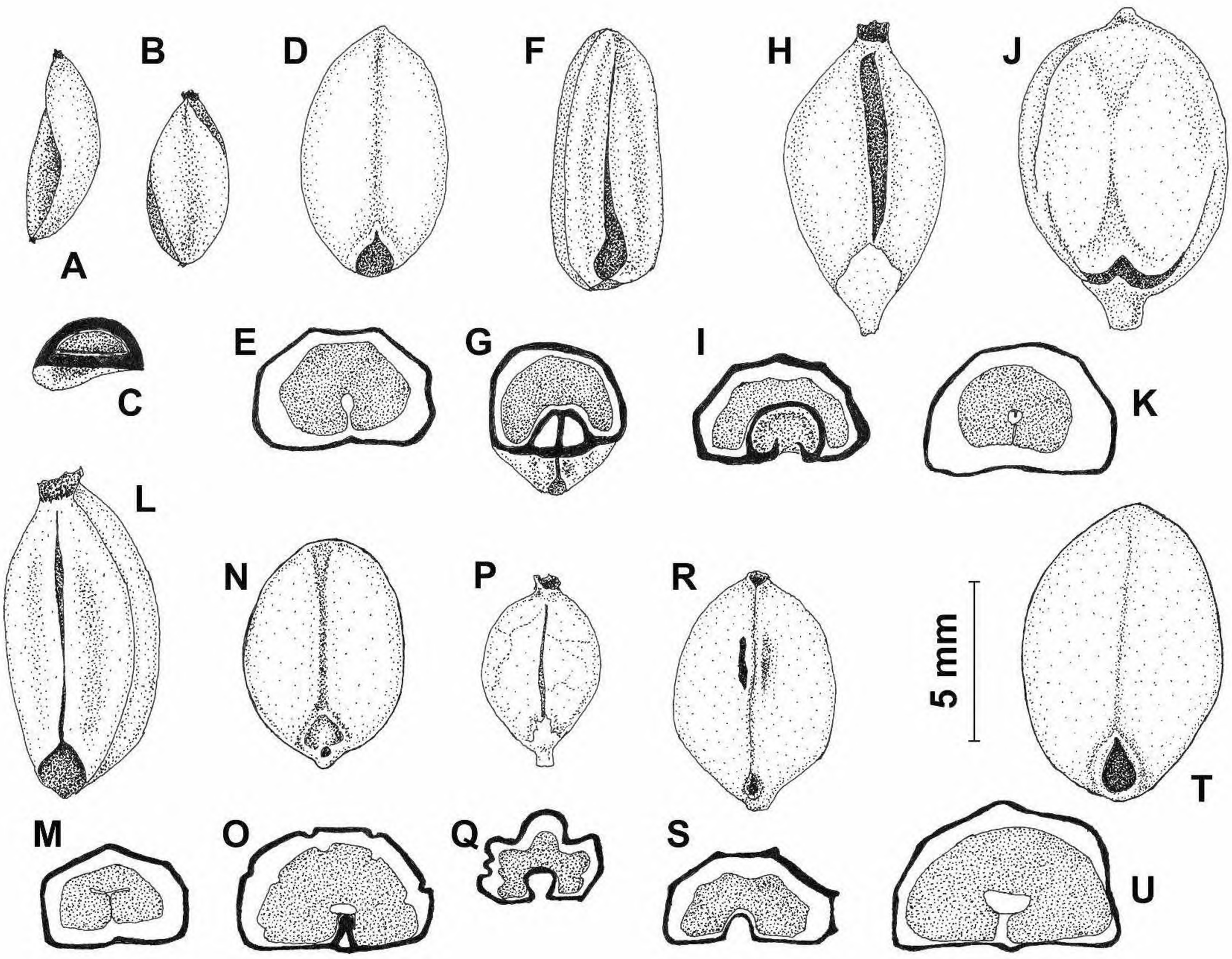


Figure 1. Pyrenes of selected *Carapichea* species, each with a view of the adaxial (i.e., ventral) face and a schematic cross-section near middle. Species order follows the text. All figures to same scale. In the schematic cross-sections, pyrene walls are in black and endosperm is stippled; these drawings are based on dried specimens, with endosperm sometimes shrunken. A–C. *Carapichea ipecacuanha* (Brot.) L. Andersson (*Ipecacuanha* group), based on *L. A. Skorupa et al. 712* (MO). —A. Pyrene side view. —B. Pyrene adaxial view. —C. Cross-section of pyrene. D, E. *Carapichea affinis* (Standl.) L. Andersson (*Carapichea* group), based on *E. Rodríguez et al. 1160* (MO). —D. Pyrene adaxial view. —E. Schematic cross-section of pyrene. F, G. *Carapichea guianensis* Aubl. (*Carapichea* group), based on *P. Acevedo et al. 5924* (MO). —F. Pyrene adaxial view. —G. Cross-section of pyrene, showing air chambers formed by pyrene wall. H, I. *Carapichea maturacensis* (Steyerm.) C. M. Taylor (*Carapichea* group), based on *B. Stein & A. Gentry 1698* (MO). —H. Pyrene adaxial view, with raphal plug still attached. —I. Cross-section of pyrene showing concave intrusion with extended margins of pyrene wall. J, K. *Carapichea ligularis* (Rudge) Delprete (*Pacimonica* group), based on *L. Andersson 1989* (MO). —J. Pyrene adaxial face. —K. Schematic cross-section of pyrene. L, M. *Carapichea pacimonica* (Müll. Arg.) C. M. Taylor (*Pacimonica* group), based on *B. Stergios et al. 16280* (MO). —L. Oblique view of adaxial pyrene face. —M. Schematic cross-section of pyrene. N, O. *Carapichea urniformis* (Steyerm.) C. M. Taylor (*Altsonii* group), based on *D. Clarke et al. 8963* (MO). —N. Pyrene adaxial face. —O. Schematic cross-section of pyrene. P, Q. *Carapichea panurensis* (Müll. Arg.) C. M. Taylor (*Panurensis* group), based on *L. Kawasaki 204* (MO). —P. Pyrene adaxial face, with raphal plug still attached. —Q. Schematic cross-section. R, S. *Carapichea tillettii* (Steyerm.) C. M. Taylor (*Panurensis* group), based on *D. Clarke et al. 10713* (MO). —R. Pyrene adaxial face. —S. Schematic cross-section of pyrene. T, U. *Carapichea adinantha* (Standl.) C. M. Taylor (*Stachyococcus* group), based on *R. Vásquez et al. 2192* (MO). —T. Pyrene adaxial face. —U. Schematic cross-section of pyrene.

yellowish brown, brown, or greenish brown color, which may be related to the chemistry of these species, but specifics of this are unknown. Drying color varies within some Rubiaceae genera (e.g., *Gaertnera* Lam.; Malcomber & Taylor, 2009), but is rather consistent and sometimes distinctive in others (e.g., *Psychotria* subg. *Psychotria*; Hamilton, 1989). The gray or blackened color found in many species of *Carapichea* is similar to that found in several species of *Psychotria* subg. *Psychotria* (e.g., *P. marginata* Sw.), but these genera are not very similar chemically (Bernhard et al., 2011).

The morphology of the stipules is useful for diagnosing and distinguishing many Psychotrieae genera (Taylor, 1996, 2005) and appears to be a diagnostic feature for *Carapichea*. The stipules of the species included here in *Carapichea* are interpetiolar, apparently lack glands on the margins and external

(i.e., abaxial) surface, and are marcescent or deciduous in a characteristic way: the margins become brown and dry, then the stipule body becomes a little indurated and sometimes also yellowed, then the stipule breaks up via fragmentation with age. These indurated fragmenting stipules are similar to those of *Margaritopsis*; however, the stipules of *Margaritopsis* are generally also glandular on the tips of the lobes and/or along the margins. *Carapichea*'s hardening and fragmenting stipules differ from those of most species of *Palicourea* s.l., although the stipules of a few species are similar in this regard (e.g., *P. palustris* A. C. Gilman & C. M. Taylor; Gilman & Taylor, 2008). In form, the stipules of *Carapichea* vary among the species from entire to deeply bilobed, and this entire range of variation is also found within a few species (e.g., *C. guianensis*). The laciniate stipules of *C. ipecacuanha* are unique within *Carapichea* although this stipule form is found in some related genera (e.g., *Rudgea*; Taylor et al., 2004).

Some details of the leaf venation vary markedly within *Carapichea*, but several of the informal species groups recognized here are characterized in part by distinctive venation arrangements. In most species of *Carapichea* the leaf venation is similar to that found widely in the Psychotrieae, with well-developed eucamptodromous or brochidodromous secondary veins, few and short but regularly developed intersecondary veins, and evident reticulated tertiary venation. However, in several *Carapichea* species the intersecondary veins are numerous and exceptionally well developed (*Pacimonica* group), while in some other species the venation is hardly evident (*Panurensis* group) or not at all visible (*Altsonii* group). No tuft or crypt domatia (Robbrecht, 1988) have been seen, although the species of the *Pacimonica* group have a line of short pubescence extending along each side of the midrib on the lower leaf surface that may have a function similar to the axillary domatia.

INFLORESCENCES AND FLOWERS

Inflorescence form is markedly variable within many genera of Rubiaceae (e.g., Petit, 1964; Steyermark, 1972; Taylor, 2001a; Malcomber & Taylor, 2009), but sometimes general characteristics are shared within a genus. The species included here in *Carapichea* share inflorescences with sessile or very shortly pedicellate flowers arranged in small to large groups, with the flowers or flower groups borne terminally on the inflorescence axes when these are developed. However, inflorescence arrangement varies widely from a single, sometimes involucrate, very compactly branched headlike (i.e., "capitate") or almost headlike (i.e., "subcapitate") structure with the floral bracts lacking to well developed, to a thyrse that is branched to several orders, with the bracts varying from developed to reduced. The inflorescence form of some *Carapichea* species changes over time: the inflorescence is typically capitate or subcapitate when the first flowers open, but becomes laxly branched to one or even two orders by the time the last fruits are maturing (e.g., *C. ligularis*, *C. tillettii* (Steyerm.) C. M. Taylor). In flower and fruit the inflorescence axes and bracts may range from green to white, or be bright pink or purple. In several species the flowers are immediately subtended by a distinctive ring of pilose or sericeous pubescence (e.g., species of the *Pacimonica* group); as noted by Steyermark (1972), similar pubescence is also found in some species of *Palicourea* s.l. (e.g., *Psychotria trichocephala* Poepp. & Endl.).

The corollas of *Carapichea* are most commonly short (4–8 mm long), white, and presumably pollinated by bees or other insects (e.g., *C. ipecacuanha*) but also vary in size (to 12–15 mm long), are variously yellow, orange, pink, or purple in color, and are pollinated apparently by butterflies or hummingbirds (e.g., *C. pacimonica* (Müll. Arg.) C. M. Taylor). The flowers of at least some species are distylous, but many species of *Carapichea* are so poorly documented that their floral biology cannot be determined.

Johansson (1992) detailed the pollen morphology of several of the species newly included here in *Carapichea* (as species of *Psychotria*) and found it to be aperturate in all of them. Johansson placed these species in two of his pollen morphological groups, group XIV with 3- to 5-colpate grains, which comprised only *C. vasivensis* (Müll. Arg.) C. M. Taylor, and group XVI, with 3- to 5-colpate, -porate, or -colporate grains, comprising *C. pacimonica*, *C. tillettii*, and about 45 other Neotropical and African species. Johansson noted that the pollen of his group XVI was variable in several features, and this particular group included species that are not all closely related and have a rather generalized pollen form; the other species of Johansson's group XVI are today classified in *Margaritopsis*, *Notopleura*, *Palicourea* s.l., *Rudgea*, *Psychotria* subg. *Psychotria*, and the tribe Lasiantheae (*Ronabea*).

FRUITS AND PYRENES

The fruits of the species included here in *Carapichea* vary from orange, red, dark red, blue, or dark purple to black, although in some species the fruits apparently pass through a red or orange immature phase and ultimately turn dark-colored or

black when ripe (e.g., *C. araguariensis* (Steyerm.) C. M. Taylor), and *C. verrucosa* reportedly has white or yellow fruits. Andersson (2002a) noted that the pyrenes of the two *Carapichea* species he studied are larger than average in his *Palicourea* group, but the species now included here have a wide range of pyrene sizes. Relatively large pyrenes are necessarily borne in relatively large fruits, so pyrene size may be correlated more with fruit dispersal of individual species than a genus-level feature.

The pyrenes of most of the species included here in *Carapichea* have a planoconvex shape, several low ribs or ridges on the abaxial (i.e., dorsal) side, and a weak to well-developed longitudinal central furrow on the adaxial (i.e., ventral) side (Fig. 1). This adaxial furrow corresponds to an adaxial invagination in the seed, similar to the general form found in *Palicourea* s.l. (Piesschaert, 2001), although in *Carapichea* species this furrow is more often widened at the base. The PGSs are positioned along the abaxial ridges, adaxially along the basal portion of the adaxial furrow, around the basal or raphal (Robbrecht, 1988) plug, or sometimes along the basal portions of the margins. Pyrene features in part characterize several of the informal species groups presented here.

The pyrenes of *Carapichea ipecacuanha*, the only species of the *Ipecacuanha* group, differ from those of other species of *Carapichea*. These are planoconvex, abaxially smooth except with one low, sharp, median ridge, adaxially flat or with a slender longitudinal thickening, and longitudinally twisted (Brazil, *L. A. Skorupa et al. 712*, MO!; Panama, *Croat 12427*, MO!, *Busey & Croat 237*, MO!; Fig. 1A–C). The twisting is gentle but clearly evident in all pyrenes seen. The adaxial ridge is weakly developed and arises from a basal thickening or plug and extends through the basal half of the pyrene. Dehiscence is via splitting along the sides of the basal plug plus a longitudinal slit that extends along the basal half of the adaxial face. These pyrenes are similar in form and dehiscence to the pyrenes of some species of *Geophila* (Piesschaert et al., 1999). The dehiscence of these pyrenes is similar to that found in the *Stachyoccoccus* group and the Bahia group, but their longitudinal twist is unique within *Carapichea*.

The pyrenes of the *Carapichea* group were first studied by Andersson (2002a, *C. guianensis*) and Piesschaert (2001: 280; *C. ligularis*, as *Psychotria ligularis*). These are notable in having a well-developed broad adaxial furrow that extends for the entire length of the pyrene and is relatively deep, generally occupying a fourth to half of the pyrene. This adaxial furrow is, however, mostly enclosed by thin, usually irregular extensions of the pyrene wall, as described in detail by Andersson (2002a). These pyrenes are similar in this well-developed adaxial furrow and its thin, irregular margins to pyrenes of some species of *Chassalia* studied by Piesschaert et al. (2001), with the open type pyrene form described there. On some pyrenes of *Carapichea guianensis*, the thin broad margins of the adaxial furrow extend to meet in the middle and then fold upward (i.e., abaxially), and at times even connect with the base of the furrow to form two cylindrical longitudinal air spaces (e.g., *C. guianensis*, Fig. 1F–G). However, the pyrenes of some other species of this same group have a shallow open adaxial furrow and well-developed basal plug (e.g., *C. affinis*, Fig. 1D–E). In these species dehiscence is through the basal or raphal aperture that is formed when the enlarged tissue plug falls away plus a slit that extends along the adaxial furrow and sometimes also along short slits on the basal portions of the margins.

In the species of the *Pacimonica* group, the pyrenes are generally similar to those of the *Carapichea* group. In particular, the pyrenes of *C. maturacensis* (Steyerm.) C. M. Taylor (Fig. 1H, I) resemble those of *C. guianensis* except the extensions of the adaxial pyrene wall cover only the furrow or are fused to create a single cylindrical air chamber (Fig. 1H, I). The pyrenes of *C. pacimonica* are similar but with only a shallow adaxial invagination (Fig. 1L, M). Piesschaert, however, described the pyrenes of *C. klugii* as adaxially concave with one median crest and two shallow grooves, which are visible on his drawing of the adaxial face of the pyrene but not in his figure D in the accompanying cross-section illustration (Piesschaert, 2001: 280, 304, fig. 8.18; as *Psychotria klugii* Standl.). These two shallow adaxial grooves apparently correspond to sculpturing around the basal plug, and Piesschaert found the pyrenes of *C. klugii* to be dehiscent variously via abaxial slits or through two marginal slits plus one abaxial slit. The pyrenes of *C. ligularis* (Fig. 1J, K) are similar to the ones Piesschaert described for *C. klugii* with dehiscence through a basal plug plus two slits along the basal parts of the margins.

The pyrenes of *Carapichea urniformis* (Steyerm.) C. M. Taylor, of the *Altsonii* group, abaxially have three or four weak angles or low longitudinal ridges and adaxially have a well-developed longitudinal central furrow that extends for the entire length of the adaxial face (Steyermark, 1972: 557, fig. 74e; as *Psychotria urniformis* Steyerm.), with a raphal plug at the basal end (Fig. 1N, O). As in the pyrenes of *C. guianensis*, this adaxial furrow is at least sometimes closed off by its thin extended margins to form a separate chamber. The mode of dehiscence of this species has not been

determined in this present study, but Piesschaert described the pyrenes of *C. urniformis* (Piesschaert, 2001: 284; as *P. urniformis*) as having "3 indistinct rounded ribs" adaxially and a "deep median groove, [and a] small endocarpal thickening above raphal opening" abaxially with the dehiscence along the abaxial ribs, although the raphal opening may also function in pyrene dehiscence. The pyrenes of the other three species of the *Altsonii* group have not been seen for this study. Piesschaert described the pyrenes of *C. altsonii* (2001: 276; as *P. altsonii* Sandwith) as having "one vague median rib" abaxially and a "conspicuous, broad median crest" adaxially, but he did not determine dehiscence mode.

The pyrenes of the *Panurensis* group are relatively small within *Carapichea* and are abaxially ridged or ribbed with a well-developed central adaxial furrow (Fig. 1P, S). They have a basal pore that is covered with a plug and sometimes also an apical pore, and dehiscence appears to be through these pores.

The pyrenes of the *Stachyococcus* group are relatively large within *Carapichea* and are dehiscent via a central adaxial furrow, a pore with a basal or raphal plug, and sometimes short basal marginal slits (Figs. 1T, U, 2C). These are similar in their PGS arrangement to the species of the Bahia group and the *Ipecacuanha* group. The pyrenes of the *Stachyococcus* group lack abaxial ridges, although the pyrenes of *C. verrucosa* are unique in *Carapichea* in their abaxial surface with verrucose ornamentation (Fig. 2C).

DISTRIBUTION AND HABITAT

Carapichea is so far only known from the Neotropics, but the worldwide Psychotrieae are not well known in many tropical regions, in particular southeastern Asia, so this genus may yet be found elsewhere. In particular, *Cephaelis stipulacea* Blume of southeastern Asia shares several characters with *Carapichea*, namely similar marcescent stipules, inflorescences with the flowers grouped into several heads that are enclosed by well-developed bracts, and relatively large pyrenes similar to those of *Carapichea guianensis* and *C. ligularis*. This species was included in *Chassalia* primarily based on its pyrene morphology by Piesschaert et al. (2001) as *Chassalia stipulacea* (Blume) Piesschaert; however, further study may show that this species is more closely related to *Carapichea*.

The majority of the species of *Carapichea* are found in the Guayana Region of northeastern South America (Berry et al., 1995) and the Amazon basin. One species, *C. lucida*, has a disjunct distribution from the rest of the genus in eastern Brazil. Several species are known mainly or only from the western Amazon basin: *C. klugii*, *C. affinis*, *C. adinantha* (Standl.) C. M. Taylor, and *C. dolichophylla* (Standl.) C. M. Taylor. Only *C. affinis* and *C. ipecacuanha* reach Central America, the former ranging to southern Costa Rica and the latter to Nicaragua.

Species of *Carapichea* are largely found at low elevations, generally 0–500 m, with only *C. affinis* ranging into premontane and lower montane vegetation (Holdridge, 1967), up to 1570 m in Ecuador and Peru. Habitat information is limited for many species, but several have been collected primarily on nutrient-poor sandy soils (*C. panurensis* (Müll. Arg.) C. M. Taylor, *C. maturacensis*), and at least one species has been collected primarily in seasonally inundated areas along nutrient-poor blackwater rivers (*C. vasivensis*). Some species are documented as widespread in noninundated sites with generalized soil types (e.g., *C. affinis*, *C. guianensis*). The mostly widely distributed species ecologically seems to be *C. klugii*, which has been collected in a variety of nutrient-poor to nutrient-rich, inundated to upland habitats.

METHODS

TAXONOMY

This work is based on study of herbarium specimens using standard techniques. Morphological terms follow Lawrence (1951). Specimens were studied from the collections of BR, COAH, F, G, MO, and NY. Specimens are identified by accession number when available, and when the specimen has no accession number, then if possible by bar code number, which is given here inside brackets to distinguish it from the accession number. Additional collection data for the specimens cited here and information about additional specimens not cited here are also available in the online database TROPICOS (<http://www.tropicos.org>), along with high-resolution digital images of some type specimens and selected reference specimens of most of the species treated here; the images can be accessed either by taxonomic name or by collector and number of the specimen that is imaged.

CONSERVATION STATUS ASSESSMENT METHODOLOGY

The study presented here is taxonomic and floristic: the objective is enumeration of the species that belong to this genus in the area of tropical Central and South America. This study is based on nonexhaustive survey of specimens collected over a number of years using varied survey methods aimed at various objectives, and the floristic information given here is a simplified presence report based on

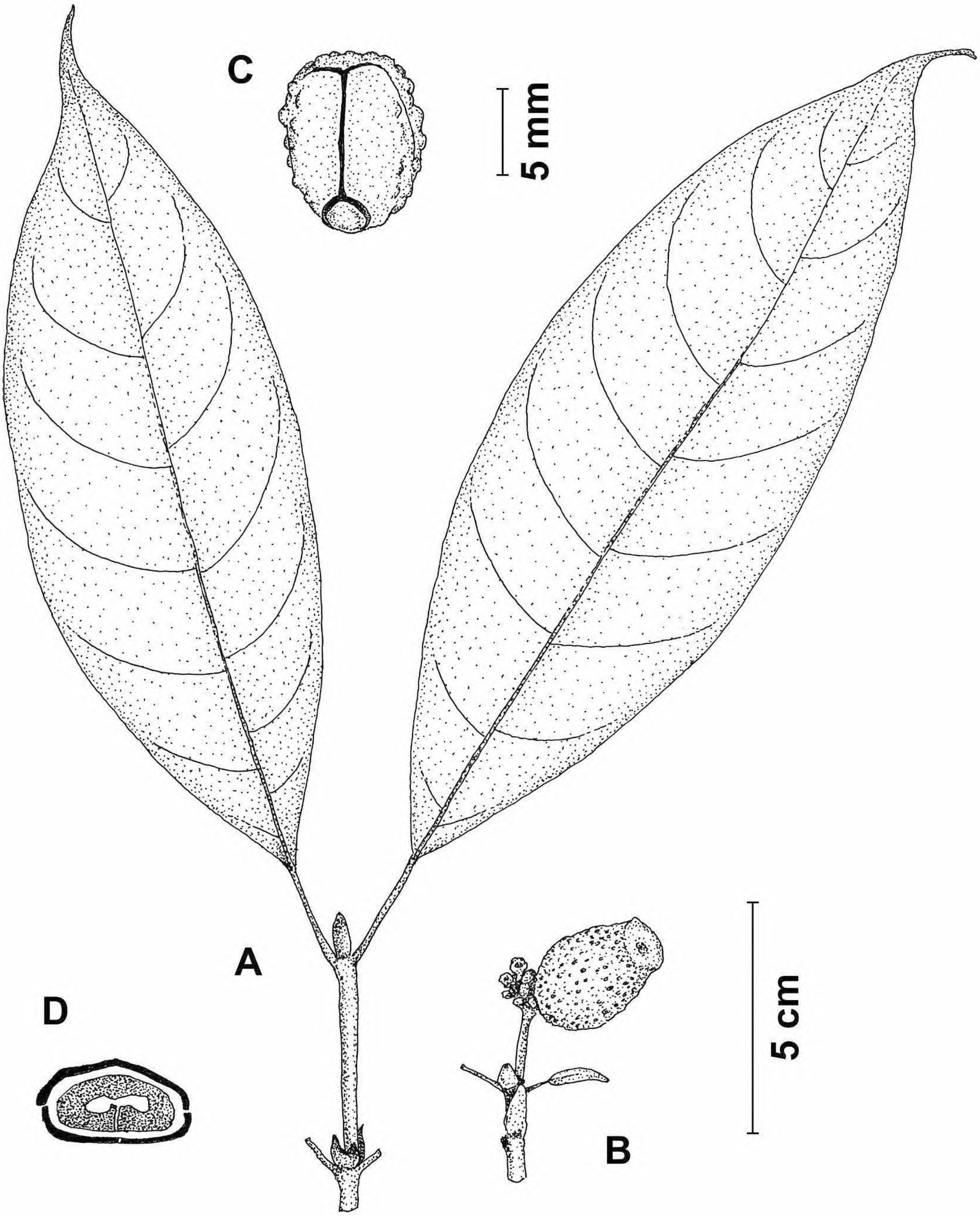


Figure 2. *Carapichea verrucosa* C. M. Taylor (*Stachyococcus* group). —A. Apical portion of vegetative stem. —B. Apical portion of stem with infructescence, with fully developed leaves removed. —C. Pyrene, based on *Mathias & Taylor 5015* (MO). —D. Schematic cross-section of pyrene, based on *Medeiros et al. 476* (MO). A, B to same 5-cm scale and based on the type *Rimachi 12346* (MO).

the available data, which are uneven and incomplete for this region (Schulman et al., 2007), and no field studies have been done targeting the occurrence of this species where it is known or expected to grow. Knowledge of the true geographic range and the population size and dynamics of a species are essential to understanding the threats to its existence and thus its actual conservation status; documenta-

tion of the existence of a species based only on museum collections does not provide data to evaluate these factors completely. A conservation assessment is provided here for this newly described species using IUCN Red List categories and criteria (IUCN, 2001) based on the totality of our current knowledge, and the basis for this assessment in the form of a map and the calculated assessment parameters is available under the corresponding species names in TROPICOS (assessment parameters are reported in the text accompanying the image). The assessment parameters were calculated using the IUCN rating tool (Moat, 2007) in ArcView GIS 3.2 (ESRI, 1999) with the grid cell size used for calculating area of occupancy (AOO) varied between 1.00 and 3.16 km depending on characteristics of the species and data (IUCN, 2011). This assessment is not being submitted to IUCN for publication in the Red List.

TAXONOMIC TREATMENT

The species of *Carapichea* are here organized into informal species groups that are morphologically separated and characterized, but these groups are not formally named. The informal groups are designated with Roman numerals, and the first two are treated in the order in which they are placed on Andersson's (2002a) phylogeny with the following groups sequenced based on morphological similarity to the previous group. Within each informal group, the species are arranged in alphabetical order. The species are numbered sequentially throughout the treatment. The species are listed alphabetically in Appendix I.

Carapichea Aubl., Hist. Pl. Guian. 1: 167, t. 64. 1775, nom. rej. versus *Cephaelis* Sw., 1788, nom. cons. *Chesnea* Scop., Intr. Hist. Nat. 119. 1777, nom. superfl. illeg. *Nettlera* Raf., Sylva Tellur. 147. 1838, nom. superfl. illeg. TYPE: *Carapichea guianensis* Aubl.

Ipecacuanha Arruda, in Koster, Trav. Brazil 497. 1816, nom. nud. Species: *Ipecacuahna officinalis* Arruda, nom. nud.

Ipecacuanha Raf., Sylva Tellur. 147. 1838. TYPE: *Ipecacuanha fusca* Raf.

Uragoga L. ex Baill., Adansonia 12: 323. 1879, nom. superfl. illeg. for *Cephaelis* Sw. TYPE: *Uragoga ipecacuanha* (Brot.) Baill. (lectotype, designated by Petit [1964: 16]).

Stachyococcus Standl., Publ. Field Mus. Nat. Hist. Bot. Ser. 13(6): 144. 1936, syn. nov. TYPE: *Stachyococcus adinanthus* (Standl.) Standl.

Psychotria ser. *Altsonii* Steyerm., Mem. New York Bot. Gard. 23: 555. 1972, syn. nov. TYPE: *Psychotria altsonii* (Sandwith) Steyerm.

Shrubs and small trees, with raphides, usually glabrous, drying greenish gray, grayish brown, yellowish brown, brown, or greenish brown; internodes weakly flattened to rounded. Leaves opposite or sometimes whorled (*Carapichea tillettii*), distichous, without domatia or with a line of pubescence along abaxial sides of midrib, venation pinnate, sometimes secondary and higher-order venation not visible (*Altsonii* group), sometimes with numerous well-developed intersecondary veins (*Pacimonica* group), sometimes apparently without intersecondary veins (some species of *Carapichea* group); stipules interpetiolar, generally persistent on distalmost nodes, with age (i.e., at lower nodes) becoming dried, starting from margins, and sometimes indurated in upper parts or throughout, then falling through fragmentation, often leaving well-developed scar or persistent hardened basal portion, apparently eglandular, adaxially glabrous, generally triangular to broadly ovate or rounded-truncate, entire, minutely bifid, shallowly to deeply 2-lobed, or sometimes deeply laciniate (*Ipecacuanha* group). Inflorescences terminal, sometimes becoming displaced to pseudoaxillary (i.e., lateral) after anthesis, sessile to pedunculate, green, white, red, pink, or purple, compactly branched and headlike (i.e., capitate) to almost headlike (i.e., subcapitate), spiciform, or thyrsiform and branched to 1 or 2 orders, with axes 2 to 4 per node, bracteate; bracts reduced (*Stachyococcus* group) to well developed, sometimes with basalmost (i.e., outermost) bracts involucral, enlarged, free or shortly to completely fused bracteoles subtending flowers reduced or sometimes replaced by glandular projections (*Altsonii* group) or pubescence (*Pacimonica* group, *Carapichea* group). Flowers bisexual, at least sometimes distylous, sessile to very shortly pedicellate; calyx limb developed, 5-lobed or sometimes truncate (*Panurensis* group, *C. pacimonica*); corolla tubular to funnelform, white, yellow, orange, salmon-pink, or purple, internally glabrous or variously pubescent, tube straight, lobes 5, valvate in bud, smooth or abaxially thickened or with hornlike appendage (*C. araguariensis*); stamens 5, inserted in corolla tube, included or exserted, anthers ellipsoid-oblong, dehiscent by longitudinal slits, pollen aperturate; ovary inferior, 2-locular, ovules 1 per locule, basal; stigmas 2, linear, included or exserted. Fruit drupaceous, subglobose to ellipsoid, fleshy, yellow, brownish yellow, orange, red, dark red, dark purple, maroon, dark blue, white, or cream, sometimes with pedicel or stipe elongating during maturation; pyrenes 2, hemispherical (i.e., planoconvex), 1-locular, bony, flat or sometimes

longitudinally twisted (*C. ipecacuanha*), dehiscent by 3 or 4 PGSs along abaxial ridges, or by a partial adaxial slit (*C. ipecacuanha*), or by a single basal-adaxial slit (*C. lucida*), or by a basal or raphal plug and sometimes also short marginal slits (*C. adinantha*, *C. verrucosa*), abaxially smooth or with 1 central crest or 3 to 5 angles or ridges, adaxially plane or with a narrow to broad, open to covered central furrow (i.e., groove) along part to all of length.

Carapichea includes at least 23 Neotropical species in understory of wet tropical forests at elevations of 50–1570 m, and has been collected from eastern Nicaragua to Bolivia, and in Venezuela, the Guianas, and eastern Brazil.

Key to Species of *Carapichea*

1a. Stipules laciniate, with 3 to 8 projections or lobes linear, 5–10 mm long; pyrenes longitudinally twisted, smooth or with a single ridge abaxially; herbs and subshrubs to 0.5 m tall with extensive rhizomes; widespread ..... *C. ipecacuanha* (species group I)

1b. Stipules entire or 2-lobed, the lobes when present triangular to linear, 5–6 mm long; pyrenes straight, smooth to angled or ridged abaxially; herbs, subshrubs, woody shrubs, or small trees, to 4 m tall, apparently not markedly rhizomatous; Costa Rica to Bolivia and eastern Brazil.

2a. Inflorescences capitate.

3a. Stipules deeply bilobed; eastern Brazil (Bahia) ..... *C. lucida* (VII)

3b. Stipules entire and truncate, rounded, obtuse, or acute to shortly bilobed; Costa Rica to Bolivia and northeastern South America.

4a. Inflorescences with bracts reduced, to 1 mm long; fruits spongy with warty surface, white to cream or brownish yellow, 15–30 mm long; pyrenes 10–20 mm long, abaxially verrucose .... *C. verrucosa* (VI)

4b. Inflorescences with developed bracts 2–70 mm long; fruits juicy with smooth surface, dark red, maroon, dark purple, dark blue, or white, 5–15 mm long; pyrenes 3–12 mm long, abaxially smooth or with longitudinal ridges.

5a. Inflorescences with external bracts 50–70 mm long, fused for more than half their length into a funnelform tube ..... *C. urniformis* (VI)

5b. Inflorescences with external bracts 8–30 mm long, free or fused for less than half their length into a cupular tube.

6a. Inflorescences enclosed by two external bracts ca. twice or more as long as remaining bracts, these external bracts ovate, lanceolate, spatulate, or pandurate, at apex acute.

7a. Inflorescences with the 2 external bracts lanceolate, spatulate, or pandurate, with peduncle 0.8–3.5 cm long; leaves of flowering branches 3.5–7 cm wide ... *C. guianensis* (II)

7b. Inflorescences with the 2 external bracts ovate, with peduncle 2–12 cm long; leaves of flowering branches 4–12.5 cm wide.

8a. Leaves of flowering branches 6–12.5 cm wide; stipules 8–15 mm long ..... *C. dolichophylla* (II)

8b. Leaves of flowering branches 4–4.3 cm wide; stipules 21–22 mm long. ..... *C. fimbriflora* (III)

6b. Inflorescences enclosed by several external bracts less than twice as long as remaining bracts, these external bracts linear, narrowly triangular, narrowly spatulate, elliptic, oblanceolate, lanceolate or ovate, at apex acute, obtuse, rounded, or truncate.

9a. Inflorescences with external bracts linear to narrowly triangular or narrowly spatulate, 1–4 mm wide; leaves with intersecondary veins well developed, with 1 to 4 intersecondary veins present between each pair of secondary veins, with 1 or more intersecondary veins more than half as long as secondary veins.

10a. Inflorescences with largest bracts narrowly triangular and 8–12 mm long ... *C. crebinervia* p.p. (III)

10b. Inflorescences with largest bracts narrowly spatulate to linear and 10–30 mm long.

11a. Outermost inflorescence bracts at base straight-sided and not sheathing; plants often drying with gray cast ..... *C. ligularis* (III)

11b. Outermost inflorescence bracts at base widened and shortly sheathing; plants often drying yellowish brown ..... *C. pacimonica* (III)

9b. Inflorescences with external bracts spatulate, elliptic, oblanceolate, lanceolate, or ovate, 5–20 mm wide; leaves with intersecondary veins not visible or few and all less than half as long as secondary veins.

12a. Leaves with secondary veins visible on adaxial surface; inflorescence with 6 to 20 external bracts ..... *C. affinis* (II)

12b. Leaves with secondary veins not visible on adaxial surface; inflorescence with 4 or 5 external bracts.

13a. Inflorescence with peduncle 9.5–17 cm long and bracts green or white often tinged with pink or purple; calyx limb subtruncate to shortly irregularly lobed ..... *C. altsonii* (IV)

13b. Inflorescence bracts with peduncle 2.5–4 cm long and bracts white; calyx limb shortly to deeply, irregularly or regularly lobed.

14a. Calyx lobes lanceolate to ovate-triangular, 0.7–1.2 mm long, acute to acuminate; corolla tube 16–19 mm long ..... *C. nivea* (IV)
14b. Calyx lobes irregular, triangular, 0.2–0.8 mm long, obtuse to rounded; corolla tube 9–11 mm long ..... *C. sandwithiana* (IV)

2b. Inflorescences with primary axis at least shortly developed and sometimes also secondary and tertiary axes developed.
15a. Inflorescences spiciform, with primary axis well developed and flowers borne in glomerules directly from it, or some flowers borne on secondary axes 1–5 mm long and much shorter than primary axis.
16a. Inflorescences shortly developed, with flowers borne at apex and 1 lower node; stipules 5–18 mm long; fruit 5–8 mm long ..... *C. panurensis* p.p. (V)
16b. Inflorescences more developed, with flowers borne at apex and at 4 to 15 lower nodes; stipules 2–5 mm long; fruit 10–15 mm long ..... *C. adinantha* (VI)
15b. Inflorescences cymose, with secondary axes and sometimes tertiary axes developed and flowers mainly borne on these, longest secondary axes 6–30 mm long and shorter than to as long as primary axis.
17a. Leaves with intersecondary veins well developed, with 1 to 4 intersecondary veins present between each pair of secondary veins, with 1 or more of these intersecondary veins more than half as long as secondary veins.
18a. Inflorescence with outermost bracts subequal or a little unequal, with the outermost bracts that subtend a group of flowers less than twice as long as next longest bracts ..... *C. crebinervia* p.p. (III)
18b. Inflorescence bracts markedly unequal, with the outermost bracts that subtend a group of flowers more than twice as long as next-longest bracts.
19a. Outermost bracts subtending flower groups 10–15 mm long ..... *C. araguariensis* (III)
19b. Outermost bracts subtending flower groups 20–25 mm long ..... *C. necopinata* (III)
17b. Leaves with intersecondary veins not visible or few and weak and all less than half as long as secondary veins.
20a. Inflorescences with bracts reduced, not covering ovaries of flowers nor enclosing groups of flowers; leaves with secondary veins not visible on abaxial surface ..... *C. panurensis* p.p. (V)
20b. Inflorescences with at least some bracts developed, covering ovaries of some or all flowers individually and/or enclosing groups of flowers; leaves with secondary veins weakly evident to clearly evident on abaxial surface.
21a. Calyx limb 2–3.5 mm long.
22a. Corolla with tube 15–16 mm long and lobes ca. 10 mm long; inflorescence with bracts equal to unequal in size ..... *C. maturacensis* (II)
22b. Corolla with tube 5–7 mm long and lobes 4–4.5 mm long; inflorescence with bracts generally similar in size ..... *C. vasivensis* (II)
21b. Calyx limb 0.8–1 mm long.
23a. Leaves drying leathery; stipules generally smooth; inflorescence with bracts 3–4 mm long; corolla with tube ca. 6 mm long and lobes ca. 3.5 mm long ... *C. tillettii* (V)
23b. Leaves drying papery; stipules generally costate; inflorescence with bracts 5–7 mm long; corolla with tube ca. 4 mm long and lobes 1.2–1.5 mm long (corolla unknown in *C. franquevilleana*).
24a. Stipules emarginate to shallowly 2-lobed when young; plants of southern Venezuela and southeastern Colombia ..... *C. franquevilleana* (II)
24b. Stipules acute to obtuse when young, though sometimes tardily splitting when old; plants of northeastern Peru ..... *C. klugii* (II)

I. *Ipecacuanha* Group

This group comprises one species found widely in lowland wet forests of Central and South America (Oliveira et al., 2010), though its native range may have been expanded by cultivation. This species is unusual in *Carapichea* in its low rhizomatous habit, deeply laciniate stipules, and longitudinally twisted pyrenes. The leaves lack acarodomatia, and the intersecondary veins, tertiary veins, and higher-order venation are not visible. This species is distylous as documented by Camargo de Assis and Giulietti (1999) and Rossi et al. (2005). The fruits are usually described by collectors as dark red but rarely as blue.

Its systematic position was controversial for many years, but its relationship to species included in *Carapichea* has been demonstrated by molecular sequence data (Andersson, 2002a; Bremer & Eriksson, 2009). This species was not treated by Steyermark (1972) in his study of Psychotrieae in northeastern South America.

1. Carapichea ipecacuanha (Brot.) L. Andersson, Kew Bull. 57: 371. 2002. Basionym: *Callicocca ipecacuanha* Brot., Trans. Linn. Soc. 6: 137. 1802. *Psychotria ipecacuanha* (Brot.) Stokes, Bot. Mat. Ned. 1: 365. 1812. *Cephaelis ipecacuanha* (Brot.) A. Rich., Bull. Fac. Med. 4: 92. 1818. *Uragoga ipecacuanha* (Brot.) Baill., Hist. Plant. 7: 370. 1880. *Evea ipecacuanha* (Brot.) W. Wight, Contr. U.S. Natl. Herb. 9: 216. 1905; *Evea ipecacuanha* (Brot.) Standl., Contr. U.S. Natl. Herb. 18: 123. 1916, isonym, nom.

inval. TYPE: Tab. 11 in Brot., Trans. Linn. Soc. 6: t. 11, 1802 (lectotype, designated by Boer & Thulin [2005 (2006): 1081]).

Ipecacuanha fusca Raf., Sylva Tellur. 147. 1838. TYPE: not designated.

Cephaelis acuminata H. Karst., Deut. Fl. 1196. 1883. *Uragoga acuminata* (H. Karst.) Farw., Druggist's Circ. 61: 175. 1917, nom. illeg., non *Uragoga acuminata* (Benth.) Kuntze, Revis. Gen. Pl. 1: 299. 1891. TYPE: Colombia. Chocó: mun. Riosucio, zona de Urabá, cerros del Cuchillo, camino de Cidon a la cumbre sureste, 50–100 m, 23 June 1988, *D. Cárdenas 2093* (neotype, designated by Boer & Thulin [2006: 1081], JAUM not seen; isoneotypes, HUA not seen, MO-4049656!).

This species is found from Nicaragua sporadically to eastern Brazil in wet forests at elevations of 0–400 m. Oliveira et al. (2010) found that the geographic distribution of this species is fragmented with markedly different levels of genetic and chemical diversity in different populations. A morphological description and illustration of this species were provided by Burger and Taylor (1993: 255, fig. 13, as *Psychotria ipecacuanha*), and a description by Taylor (2001b: 2265–2266, as *P. ipecacuanha*). The morphological variation of this species in Brazil was extensively documented and illustrated by Camargo de Assis and Giulietti (1999, as *P. ipecacuanha*), and its phenology was studied by Rodrigues et al. (1995).

This species has long been the principal source of the vomitory drug ipecac, which is derived from its well-developed rhizomes. Boer and Thulin (2005) listed various pharmaceutical names that have been used for this species.

II. *Carapichea* Group

This group includes seven species found in lowland wet to seasonal forests at elevations of 20–1570 m, from southern Central America to Bolivia and through the Guianas and the Amazon basin to southeastern Brazil. These species share well-developed, entire to bilobed stipules, a usually grayish or brownish gray drying color, capitate to branched inflorescences with well-developed peduncles and well-developed bracts, and usually purple to blue-black fruits. The leaves have well-developed secondary veins but lack visible intersecondary veins and often the tertiary and higher-order venation are not visible. Acarodomatia appear to be lacking. The stipules are generally ovate to triangular-ligulate, and variously entire, minutely bifid, or bilobed, sometimes with this variation all found in the same species (e.g., *C. guianensis*). The inflorescence bracts are generally equal in size or have a regular gradation from largest to smallest except in *C. guianensis* and *C. dolichophylla*, which have a pair of markedly larger outermost bracts that are twice or more as large as the next largest bracts. The inflorescence bracts are generally described as green, white, pink, red, purple, or lilac during flowering and as green, red, or purple during fruiting. The flowers are generally subtended by dense sericeous or lanose pubescence and are apparently distylous. The corollas are white and often have abaxial thickenings or horns on the lobes. The fruits are described as red-orange maturing to black (*C. guianensis*, *Clarke 4366*, MO!) or maturing to orange, dark red, dark purple, violet, or purple-black.

This species group includes the type of *Carapichea*, *C. guianensis*, which has been treated taxonomically in different ways. Steyermark (1972, 1974) included these plants as one of two varieties of *Psychotria ligularis*, as *P. ligularis* var. *carapichea*. However, Delprete (2001) noted that Steyermark's varieties are better regarded as two different species and the other, *C. ligularis* (= *P. ligularis* var. *ligularis* of Steyermark) is here included as a species belonging to a different group, the *Pacimonica* group. Steyermark classified *C. guianensis* (1972; as *P. ligularis* var. *carapichea*) in his *Psychotria* sect. *Cephaelis* (Sw.) Müll. Arg. and its *Psychotria* ser. *Cephaelis* Steyerm. (Steyermark [1972: 668] here appears to have incorrectly regarded his *Psychotria* ser. *Cephaelis* as an autonymic name because it included the type species of the name of its higher taxon, *Psychotria* sect. *Cephaelis*; however, this section does not include the type of the genus, and thus is not an autonym. Even though he treated this series as an autonym, Steyermark did provide a Latin diagnosis and designated a type, so he is the author of this name.) Three of the species included in the *Carapichea* group, *C. franquevilleana* (Müll. Arg.) C. M. Taylor, *C. vasivensis*, and *C. maturacensis*, were classified by Steyermark (1972) in his unnamed and undiagnosed *Psychotria* sect. 7 (1972: 574) and its unnamed and undiagnosed *Psychotria* ser. A (1972: 574) together with another species that is not transferred to *Carapichea*, *P. wurdackii* Steyerm.

2. Carapichea affinis (Standl.) L. Andersson, Kew Bull. 57(2): 371. 2002. Basionym: *Cephaelis affinis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(3): 184. 1930. TYPE: Peru. Loreto: betw. Yurimaguas & Balsapuerto, 26–31 Aug. 1929, *E. P. Killip & A. C. Smith 29329* (holotype, US-1356290, US digital image!; isotype, F-612034, F digital image!).

Cephaelis borucana Ant. Molina, Ceiba 4: 31. 1951. *Psychotria borucana* (Ant. Molina) C. M. Taylor & W. C. Burger, Monogr. Syst. Bot. Missouri Bot. Gard.

45: 1258. 1993. TYPE: Costa Rica. Puntarenas: cantón de Osa, near Esquinas Experimental Station, area betw. Río Esquinas & Palmar Sur de Osa, 200 ft., 11 May 1950, *P. H. Allen 5340* (holotype, US-2215926 digital image!; isotypes, F-174638 digital image!, US-2086253 digital image!).

This species is known from wet lowland, premontane, and lower montane forests at elevations of 20–1570 m, in southern Costa Rica and from the western Amazon basin of Colombia to Bolivia and into western Brazil. A modern description and illustration of this species were presented by Burger and Taylor (1993: 236, fig. 17; as *Psychotria borucana*) and a description by Taylor (1997b: 626, as *P. borucana*). The inflorescences of this species are densely capitate but often become somewhat lax as the fruits mature, with the receptacle broadening and sometimes the inflorescence axes shortly developing. This species is similar to *Carapichea dolichophylla*; see additional comments about their separation in the discussion of that species.

3. Carapichea dolichophylla (Standl.) C. M. Taylor, Fl. Ecuador 79: 6. 2006. Basionym: *Cephaelis dolichophylla* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4(8): 334. 1929. *Psychotria dolichophylla* (Standl.) C. M. Taylor, Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1258. 1993. TYPE: Peru. Loreto: prope Yurimaguas ad flumen Huallaga, Peruviae orientali, May 1855, *R. Spruce 3876* (holotype, K[000006657], K digital image!; isotype, K[000006656], K digital image!).

This species is known from wet forests at elevations of 100–900 m in the western Amazon basin, from Colombia to Bolivia and western Brazil. A modern description was presented by Taylor (1997b: 627; as *Psychotria dolichophylla*). This species is similar to *Carapichea affinis*, which has a broader geographic range and is more commonly collected. These two species are distinguished by features of the inflorescence: in *C. dolichophylla* the bracts are acute to obtuse and clearly angled at the apex, and the inflorescences are fully enclosed by a pair of external bracts that are markedly larger than the other bracts and described as green, pink, or usually red in flower and green to occasionally purple or usually red in fruit; while in *C. affinis* the bracts are broadly obtuse to rounded at the apex, and the inflorescence is surrounded by two or three pairs of bracts, with no pair of bracts completely enclosing the head nor markedly larger than the others, and the inflorescence bracts are described as green or infrequently pink in flower and becoming purple in fruit.

Two specimens of Spruce's collection #3876 deposited at K are available for study as digital images. The specimen annotated in Standley's handwriting as "*Cephaelis dolichophylla* Standl. Type" is here considered the holotype, and the duplicate specimen that has no annotation by Standley is considered an isotype.

4. Carapichea franquevilleana (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Psychotria franquevilleana* Müll. Arg., Fl. Bras. 6(5): 325. 1881. *Uragoga franquevilleana* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Venezuela. Amazonas: in regione Rio Negro ad flumen Pacimoni in montanis, Feb. 1854, *R. Spruce 3378* (holotype, P in Herbarium Franqueville not seen, P in Herbarium Franqueville as photo F neg. #37238 at MO!; isotypes, G!, G as photo F neg. #25785 at MO!, K[00043841], K digital image!).

This species is known from lowland vegetation at elevations of ca. 250 m in southern Venezuela and southeastern Colombia. The collection locality was ascribed to Brazil by Spruce, but Steyermark (1972: 580) clarified that it is today in Venezuela. In addition to the locality information given in the protologue, cited above, the label adds the specific locality "in sylvis pedem montis Imei."

This species is poorly known and is treated provisionally here following Steyermark (1972, 1974). It was originally described as based on a specimen without flowers or fruits, with details of the flowers added by Steyermark based apparently on a single specimen from Colombia (*H. García-Barriga 13939*, no herbarium cited, not seen). A morphological description was presented by Steyermark (1974: 1444–1446), and later re-stated by Taylor et al. (2004: 739). Steyermark's description expanded the morphological variation included in this species, in particular in the calyx limb that he noted ranges to repand-truncate with rounded projections, while the protologue described the calyx limb as truncate, the condition found on the type collection. Steyermark also described the form of the corollas, but their size is still unknown.

In general aspect *Carapichea franquevilleana* is similar to *C. vasivensis*, which is known from the same region in Venezuela. Steyermark (1972: 580) distinguished *C. franquevilleana* by its glabrous inflorescences with secondary axes verticillate in contrast to pubescent inflorescences with paired axes in *C. vasivensis*. Steyermark confused *C. vasivensis in herb.* with *C. maturacensis*, but both of these differ in their pubescent inflorescences from *C. franquevilleana*.

Carapichea franquevilleana is also similar, including in the glabrous inflorescences of similar form, to *C. klugii* of the western Amazon basin; these species are separated here provisionally as discussed under *C. klugii*.

5. Carapichea guianensis Aubl., Hist. Pl. Guiane 1: 168, tab. 64. 1775. *Callicocca guianensis* (Aubl.) J. F. Gmel., Syst. Nat. 2(1): 372. 1791; as "gujanensis." *Tapogomea carapichea* Poir., Encycl. 7: 587, tab. 152, fig. 3. 1806, nom. superfl. illeg. *Cephaelis involucrata* Willd., Sp. pl. 1: 979. 1798, nom. superfl. illeg. *Carapichea aubletii* DC., Prodr. 4: 536. 1830, nom. superfl. illeg. *Nettlera guianensis* (Aubl.) Raf., Sylva Tellur. 147. 1838. *Uragoga involucrata* (Willd.) Kuntze, Revis. Gen. Pl. 2: 956. 1891, nom. superfl. illeg. *Uragoga guianensis* (Aubl.) Pulle, Enum. Vasc. Pl. Surinam 446. 1906. *Cephaelis guianensis* (Aubl.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4(8): 335. 1929. *Psychotria ligularis* var. *carapichea* Steyerm., Mem. New York Bot. Gard. 23: 676. 1972. *Psychotria carapichea* (Steyerm.) Delprete, Brittonia 53: 401, fig. 2. 2001, non *Psychotria guianensis* (Aubl.) Raesch., 1796. TYPE: French Guiana. Dans les grandes forêts qui aboutissent à la crique des Galibis, en fleur et en fruit Mai, *Aublet s.n.* (holotype, BM not seen).

Psychotria galbaoensis Steyerm., Brittonia 33: 387. 1981. TYPE: French Guiana. Pente nord-est des monts Galbao, a 10 km au SO de Saül, 500–600 m, 11 Mar. 1975, *J. J. de Granville 2383* (holotype, VEN not seen; isotypes, CAY not seen, MO-2798770!, MO-3332374!).

This species is known from wet forests at elevations of 150–710 m in Guyana, Surinam, French Guiana, and northern Brazil. Its systematic relationships were not clear until *Carapichea* was recognized in its modern circumscription (Andersson, 2002a). The flowers described and seen resemble the short-styled form of distylous flowers. The pyrenes sometimes have two adaxial longitudinal chambers, an unusual form. A recent description and illustration were presented by Boom and Delprete (2002; as *Psychotria carapichea*), and that same illustration was also published by Delprete (2001: 402, fig. 2; also as *P. carapichea*).

Steyermark (1972) classified these plants as a variety of *Psychotria ligularis*, which he called *P. ligularis* var. *carapichea*. He subsequently described *P. galbaoensis* based on plants from the type region of *Carapichea guianensis*, without contrasting his new species to *P. ligularis* var. *carapichea*. Delprete (2001, 2003) noted that Steyermark's varieties of *P. ligularis* are better treated as two separate species and that *P. galbaoensis* was a synonym of *C. guianensis* and published the name *P. carapichea* (Steyerm.) Delprete for *P. ligularis* var. *carapichea*. Delprete's name was originally published (2001) as "*P. carapichea* (Poir.) Delprete," with *Tapogomea carapichea* Poir. as the basionym. However, Poiret's name is illegitimate and thus not available as a basionym. Therefore, *P. carapichea* could have been considered a replacement name authored solely by Delprete, but Delprete subsequently (2003) corrected the authorship of this name to cite *P. ligularis* var. *carapichea* Steyerm. as the basionym and Steyermark as the parenthetical author. The typification cited here for *C. guianensis* follows Delprete (2003).

6. Carapichea klugii (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria klugii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(5): 377. 1931. TYPE: Peru. Loreto: in forest, Mishuyacu near Iquitos, alt. 100 m, Jan. 1930, *G. Klug 835* (holotype, F-612590; isotype, NY[00132715], NY digital image!).

This species is known from both terra firme and seasonally inundated wet vegetation on various substrates, including very often white sands, at elevations of 122–200 m in the western Amazon basin of Peru and perhaps southern Colombia. This species shows some variation in the drying color of its specimens, which generally are either yellowish brown or dark brownish gray. However, these two drying-color forms are morphologically indistinguishable, and both have been collected at several sites (e.g., Peru, Mishana, Río Nanay: *F. Ayala 5995*, *M. Rimachi Y. 2239*, yellowish brown; *F. Ayala et al. 3207*, *M. Rimachi Y. 4167*, brownish gray); further study will be necessary to understand this variation. The inflorescences vary in size and form in this species, apparently with age: they are generally rather small and densely bracteate in flower, then the axes become more elongated and robust and the bracts fall off as the fruits develop.

Carapichea klugii is similar to *C. franquevilleana*. These two species differ in their stipule shape, emarginate to bilobed in *C. franquevilleana* in contrast to acute to obtuse in *C. klugii*, and they are apparently geographically separated, with *C. franquevilleana* found in the northern and northeastern Amazon basin and *C. klugii* in the western Amazon basin. Stipule shape is highly variable within some other species of *Carapichea* (e.g., *C. guianensis*) and may not be a good indication of species distinctions but may be consistent within some species. No other morphological differences are

evident between these; *C. franquevilleana* is very poorly known, and the area between their known ranges is poorly explored botanically. Therefore, these species are provisionally separated here.

7. Carapichea maturacensis (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria maturacensis* Steyerm., Mem. New York Bot. Gard. 23: 578, fig. 78. 1972. TYPE: BRAZIL. Amazonas: betw. Missão Salesiana & Serra Pirapucú, on Rio Maturacá, 50–400 m, 15 Jan. 1966, *N. T. Silva & U. Brazão 60842* (holotype, NY[00132736], NY digital image!).

This species is found in scrubby or seasonal lowland vegetation at elevations of 50–400 m on nutrient-poor, often sandy soils in southern Venezuela and adjacent northern Brazil. A description and illustration were presented by Steyermark (1974: 1442–1444, fig. 236; as *Psychotria maturacensis*) and a description by Taylor et al. (2004: 746–747; as *P. maturacensis*). This species has sometimes been confused with *Carapichea vasivensis*, which is similar in general morphology but differs markedly in its corolla size, as outlined in the Key to Species, and also apparently in habitat.

8. Carapichea vasivensis (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Mapouria vasivensis* Müll. Arg., Flora 59: 460, 466. 1876. *Uragoga vasivensis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 963. 1891. *Psychotria vasivensis* (Müll. Arg.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7(4): 461. 1931. TYPE: Venezuela. Amazonas: ad flumen Casiquiare, Vasiva et Pacimoni, 1853–1854, *R. Spruce 3334* (holotype, M not seen; isotypes, C not seen, C as photo F neg. #22854 at MO!, G!, NY[00132243], NY digital image!).

This species is known from wet vegetation of seasonally inundated riversides at elevations of 100–150 m in southern Venezuela. The collection locality was ascribed to Brazil by Spruce, but Steyermark (1972) clarified that it is today in Venezuela. A description and illustration were presented by Steyermark (1974: 1436–1439, fig. 234; as *Psychotria vasivensis*) and by Taylor et al. (2004: 762, fig. 587; also as *P. vasivensis*). This species has sometimes been confused with *Carapichea maturacensis*, which is similar in its general morphology but differs markedly in its corolla size, with the tube 15–16 mm long and the lobes ca. 10 mm long in *C. maturacensis* in contrast to the tube 5–7 mm long and the lobes 4–4.5 mm long in *C. vasivensis*; also *C. maturacensis* is apparently found in wet vegetation in seasonally inundated habitats.

III. *Pacimonica* Group

This group comprises six species found in wet lowland to premontane vegetation at 50–800 m in northeastern South America. These species share a distinctive yellowish gray or gray-brown drying color, leaves with numerous well-developed intersecondary veins and the tertiary and quaternary venation hardly or not visible, relatively short truncate to broadly 2-lobed stipules, well-developed peduncles, and subcapitate to shortly branched inflorescences with green bracts of markedly different lengths with the longest bracts narrowly ligulate to linear, except in *Carapichea fimbriflora* (Steyerm.) C. M. Taylor where they are broader. The leaves lack tufted acarodomatia in the abaxial axils of the secondary veins, but abaxially there is usually a line of short pilosulose pubescence along each side of the midrib, which may serve a similar function. *Carapichea pacimonica* and *C. araguariensis* have distylous flowers; the floral biology of the other species is unknown. The corollas are described as white, salmon-pink, orange, or purple, and their lobes usually have well-developed abaxial thickenings or horns. The mature fruits are reported to be red, yellow, or most often orange and are often borne on stipes, which develop as the fruits mature.

Two of the species included here, *Carapichea araguariensis* and *C. pacimonica*, were classified by Steyermark (1972; as *Psychotria araguariensis* Steyerm. and *P. pacimonica* Müll. Arg., respectively) in *Psychotria* subg. *Heteropsychotria* and in his unnamed and undiagnosed *Psychotria* sect. 7 (1972: 574), and its unnamed and undiagnosed *Psychotria* ser. C (1972: 588) along with several other species that apparently do not belong to *Carapichea*. Steyermark classified *C. ligularis* (1972; as *P. ligularis*) in *Psychotria* sect. *Cephaelis* ser. *Cephaelis* along with *C. fimbriflora* (Steyermark, 1981; as *P. fimbriflora* Steyerm.). As discussed previously for the *Carapichea* group, Steyermark circumscribed *P. ligularis* to include two varieties that are here considered to represent separate species, *C. ligularis* of this species group and *C. guianensis* of the *Carapichea* group. Steyermark's species *P. fimbriflora* is poorly known and is provisionally classified here based on Steyermark's note that this species is most closely related to *P. ligularis*; however, he did not specify to which variety of *P. ligularis*. These two varieties or species differ in the pattern of leaf venation and the pubescence of the lower leaf surface, and although Steyermark did not describe

the leaf venation of *P. fimbriflora* he did note that its leaves abaxially have a line of puberulous pubescence along each side of the midrib, which is found in *C. ligularis* but not in *C. guianensis*.

9. Carapichea araguariensis (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria araguariensis* Steyerm., Mem. New York Bot. Gard. 23: 588. 1972. TYPE: Brazil. Amapa: Rio Araguari, vic. Camp 12, 1°11′N, 52°8′W, 20 Sep. 1961, *J. M. Pires, W. Rodrigues & G. C. Irvine 51371* (holotype, NY[00152398], NY digital image!).

This species is known from wet forests on terra firme at elevations of 50–125 m in northern Brazil. A description of this species was presented by Taylor et al. (2004: 595; as *Psychotria araguariensis*), and it was illustrated by Campos and Brito (1999: 627, 639; misidentified as *P. pacimonica*). *Carapichea araguariensis* is similar to *C. necopinata* (Standl.) C. M. Taylor, which is poorly known and separated provisionally here from *C. araguariensis* based on differences in the inflorescence bracts: the outermost bracts of the flower groups are 10–15 mm long in *C. araguariensis* in contrast to 20–25 mm long in *C. necopinata*.

10. Carapichea crebrinervia (Standl.) C. M. Taylor, comb. nov. Basionym: *Cephaelis crebrinervia* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 188. 1936. TYPE: Brazil. Pará: in silvis non inundatis loco Antonio Lemos prope flumen Tajapuru aestuarii amazonici, 27 Sep. 1919, *A. Ducke 15351* (holotype, B, destroyed, B as photo F neg. #49863 at F digital image!).

This species is known from seasonally flooded lowland wet forests in northern Brazil, most often near the Amazon River. It has been collected infrequently and is not well known. Additional study is needed before its typification can be clarified.

11. Carapichea fimbriflora (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria fimbriflora* Steyerm., Brittonia 33: 386. 1981. TYPE: Brazil. Amazonas: Operacão Juruá-Ponto 86-SC-18-SC, 14 Nov. 1975, *B. S. Pena* (holotype, VEN-134383, VEN digital image!).

This species is known only from the type collection, from lowland wet forests on terra firme in northern Brazil. The outermost bracts of the inflorescence were described as ovate-lanceolate and are broader than long, ca. 15 mm long and ca. 18 mm wide, in contrast to the very narrow bracts found in the other members of this species group. The flowers are reported in the protologue to be purple. On the digital image of the holotype, the inflorescence has broken off the peduncle and is not shown and may be lost.

12. Carapichea ligularis (Rudge) Delprete, Brittonia 55: 89. 2003. Basionym: *Schradera ligularis* Rudge, Pl. Guian. 1: 29, tab. 45. 1805. *Cephaelis ligularis* (Rudge) DC., Prodr. 4: 533. 1830. *Uragoga ligularis* (Rudge) Kuntze, Revis. Gen. Pl. 2: 961. 1891. *Psychotria ligularis* (Rudge) Steyerm., Mem. New York Bot. Gard. 23: 675. 1972. TYPE: Guyana. S. loc., *E. Rudge s.n.* (lectotype, designated by Delprete [2001: 399], P not seen).

This species is known from wet forests at elevations of 100–800 m in Guyana, Surinam, French Guiana, and northern Brazil. The only record for Guyana appears to be the type collection. A recent description and illustration were provided by Boom and Delprete (2002; as *Psychotria ligularis*), and that same figure was also published by Delprete (2001: 400, fig. 1; also as *P. ligularis*) who clarified its taxonomic status.

13. Carapichea necopinata (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria necopinata* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 242. 1936. TYPE: Brazil. Amazonas: Cucuhy, Río Negro, ca. 120 m, Feb. 1930, *E. G. Holt & W. Gehriger 386* (holotype, F-625063, F digital image!; isotype, G!).

This species is known only from the type collection in lowland northern Brazil. Its elevational range and habitat (i.e., terra firme vs. flooded forest) were not recorded, and its mature flowers are unknown. This name was synonymized with *Carapichea pacimonica* by Steyermark (1972; both as *Psychotria*), but these species are separated here as outlined in the discussion of *C. pacimonica*. *Carapichea necopinata* is also similar to *C. araguariensis*, and their separation is outlined in the discussion of this last species.

14. Carapichea pacimonica (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Psychotria pacimonica* Müll. Arg., Fl. Bras. 6(5): 337. 1881. *Uragoga pacimonica* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Venezuela. Amazonas: in regione superiore Rio Negro ad flumen Pacimoni, Feb. 1854, *R. Spruce 3445* (holotype, M not seen; isotypes, G!, G as photo F neg. #25816 MO!, K[000432482], K digital image!).

This species is known from seasonally flooded wet forests at elevations of 100–160 m in northern Brazil and southern Venezuela. The type locality of this species was attributed to Brazil by Spruce, but its actual location in Venezuela was clarified by Steyermark (1972: 589). A description and illustration of this species were provided by Steyermark (1974: 1454–1457, fig. 240; as *Psychotria pacimonica*) and a description by Taylor et al. (2004: 750; also as *P. pacimonica*). However, the illustration presented for this species by Campos and Brito (1999: 627, 639) actually depicts *Carapichea araguariensis*. The leaves of *C. pacimonica* are notably rather thick-textured and often shiny. This species is similar to *C. ligularis*, which differs in its outermost inflorescence bracts that are not sheathing at the base in contrast to the sheathing bracts of *C. pacimonica*. *Carapichea pacimonica* is also similar to *C. crebrinervia*, which differs in its outermost inflorescence bracts that are narrowly triangular and not markedly longer than the remaining bracts in contrast to the outermost inflorescence bracts sheathing and twice or more as long as the remaining bracts in *C. pacimonica*.

Steyermark synonymized *Carapichea necopinata* with *C. pacimonica* (1972: 589; both as *Psychotria*), and Delprete (2001) agreed. Steyermark combined these species based on their similar inflorescence arrangement, pubescence, and corolla form. However, with more specimens now available, *C. necopinata* can be separated from *C. pacimonica* in its inflorescences with the secondary axes at least shortly developed and its habitat in terra firme forest in contrast to the inflorescences capitate in flower although sometimes becoming subcapitate in fruit and a habitat in seasonally flooded areas in *C. pacimonica*. Neither of these species is well documented, and Steyermark (1972) himself did not fully incorporate the morphological variation in inflorescence arrangement into his treatment: *C. pacimonica* was keyed there, as *P. pacimonica*, only as having capitate inflorescences, even though Steyermark elsewhere mentioned that this species had branched inflorescences. In practice *C. pacimonica* has been more often confused with *C. araguariensis*, as discussed under this last species.

IV. *Altsonii* Group

This group comprises four rather poorly known species found in wet lowland to lower montane escarpment forests at elevations of 80–1100 m in northeastern South America. These species share a distinctive brown drying color, relatively large leaves, broad interpetiolar stipules, capitate inflorescences with four to six well-developed involucral bracts, and shortly pedicellate flowers that lack bracts but are subtended by glandular projections of the inflorescence receptacle and/or pedicel. This inflorescence arrangement is unusual if not unique in Neotropical Psychotrieae. The leaves lack acarodomatia. Flowers have been described only for *Carapichea sandwithiana* (Steyerm.) C. M. Taylor, and although their biology is unknown, they are similar to the long-styled form of distylous species. The fruits of *C. urniformis* are reported to be bluish purple; the mature fruit color is apparently unknown for the other species.

Carapichea altsonii, *C. nivea* (Sandwith) C. M. Taylor, and *C. sandwithiana* are similar morphologically, sharing an apparently unbranched succulent habit, leaves with the venation not visible adaxially, rounded thin-textured stipules, and pedunculate inflorescences. In general aspect they resemble species of *Notopleura* subg. *Notopleura*, and Steyermark considered all the species of the *Altsonii* group related to *Notopleura*. Taylor et al. (2004) followed him and included *C. sandwithiana* in *Notopleura*, but, as detailed in the introduction, these species do not have the characters that diagnose *Notopleura*. *Carapichea urniformis* differs from the other three species of this group in its leaves with well-marked secondary and higher-order venation and its subsessile inflorescences.

15. Carapichea altsonii (Sandwith) C. M. Taylor, comb. nov. Basionym: *Cephaelis altsonii* Sandwith, Bull. Misc. Inform. Kew 1931: 475. 1931. *Psychotria altsonii* (Sandwith) Steyerm., Mem. New York Bot. Gard. 23: 555. 1972. TYPE: Guyana. Macreba Falls, Kurupung River, Mazaruni River, Aug. 1925, *R. A. Altson 322* (lectotype, designated here, K[000174497], K digital image!; isolectotype, K[000174398], K digital image!).

This species is known from wet forests at elevations of 80–400 m in Guyana. It has been collected infrequently, but was recently found again in the type locality (*B. Hoffmann et al. 2050*, MO!). This species differs from both *Carapichea nivea* and *C. sandwithiana* in its well-developed peduncles, 9.5–17 cm long, and inflorescence bracts green or white often tinged with pink or purple in contrast to the peduncles 2.5–4 cm long and the bracts white in the other two species.

16. Carapichea nivea (Sandwith) C. M. Taylor, comb. nov. Basionym: *Cephaelis nivea* Sandwith, Bull. Misc. Inform. Kew 1939: 551. 1939. *Psychotria nivea* (Sandwith) Steyerm., Mem. New York Bot. Gard. 23: 556. 1972. TYPE:

Guyana. Potaro River, Amatuk portage, on sandstone, 31 Aug. 1937, *N. Y. Sandwith 1249* (holotype, K[000174488], K digital image!; isotypes, K[000174489], K digital image!, NY-2747, NY digital image!).

This species is known from wet lowland and escarpment forests at elevations of 274–610 m in Guyana, where it has been collected infrequently. It is similar to *Carapichea altsonii*, but can be separated by its shorter peduncles, 2.5–4 cm long, inflorescence bracts flushed with white, and yellow corollas in contrast to peduncles 9.5–17 cm long and both the bracts and corollas purple in *C. altsonii*. *Carapichea nivea* is also similar to *C. sandwithiana*, but can be separated by its corollas with the tube 16–18 mm long in contrast to 9–11 mm long in *C. sandwithiana*.

Two specimens deposited at K are available for study as digital images. The specimen that has complete label data and bears the notation "Typus" in Sandwith's handwriting is here regarded as the holotype; the duplicate specimen there of this same collection that has only partial label data and no annotation as a type is considered an isotype.

17. Carapichea sandwithiana (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Cephaelis sandwithiana* Steyerm., Mem. New York Bot. Gard. 17(1): 428, fig. 42. 1967. *Psychotria sandwithiana* (Steyerm.) Steyerm., Mem. New York Bot. Gard. 23: 555. 1972. *Notopleura sandwithiana* (Steyerm.) C. M. Taylor, Fl. Venez. Guayana 8: 663. 2004. TYPE: Venezuela. Bolívar: along Río Framela, Cerro Pitón, Cordillera Epicara, Alto Río Cuyuni, Río Chicanán, 400 m, 3 Sep. 1962, *B. Maguire, J. A. Steyermark & C. K. Maguire 53562* (holotype, VEN-63029, VEN digital image!).

This species is so far known only from the type collection from wet forest at an elevation of ca. 400 m in southern Venezuela. The description presented by Taylor et al. (2004; as *Notopleura sandwithiana*) was based entirely on the protologue. This species was included in *Notopleura* by Taylor et al. (2004) based on the protologue figure that showed the inflorescence borne at the apical node alongside young leaves emerging from the stem apex, which was misinterpreted to indicate a pseudoaxillary position that supported inclusion of this species in *Notopleura*. However, further study of the species of the *Altsonii* group shows that the inflorescences are solitary and terminal and later sometimes displaced to pseudoaxillary by subsequent growth from an axillary bud but not consistently pseudoaxillary at several nodes along the stem as in *Notopleura* (Taylor, 2001a). *Carapichea sandwithiana* is similar to *C. altsonii* and *C. nivea*; its distinctions from these are summarized in the discussions of each of the other two species.

18. Carapichea urniformis (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria urniformis* Steyerm., Mem. New York Bot. Gard. 23: 556, fig. 74. 1972. TYPE: Guyana. Upper Mazaruni River basin, Mt. Ayanganna, in forest below talus along NE side, 800–900 m, 1 Aug. 1960, *S. S. Tillett, C. L. Tillett & R. Boyan 45008* (holotype, NY[00132855], NY digital image!).

This species is known from wet escarpment forests at elevations of 712–1100 m on Mt. Ayanganna in Guyana. It is notable for its capitate inflorescences enclosed by large red bracts that are fused into a vase-shaped funnelform structure. It has been collected infrequently but was found as recently as 2001 (*D. Clarke et al. 2963*, MO!).

V. *Panurensis* Group

This group comprises two species found in wet forests at elevations of 100–1570 m in the Guianas and northern Brazil. These species share stiff-textured leaves, well-developed ovate stipules, and inflorescences that are spiciform or branched to one or two orders and have relatively short bracts. Their pyrene morphology is varied: that of *Carapichea tillettii* is similar to that of some other species of *Carapichea*, while the pyrenes of *C. panurensis* are unlike any other species of *Carapichea* in their well-developed abaxial ribs. The leaves lack acarodomatia, and the secondary, intersecondary, and tertiary leaf venation is barely or not visible in both species. The stipules of *C. panurensis* are entire, whereas those of *C. tillettii* are bilobed. The bracts subtending the flower groups or secondary inflorescence axes are generally reduced; the bracts subtending the flowers are barely equal to or usually shorter than the ovary of the flowers. The flowers of both species are subtended by a ring or tuft of sericeous or pilose pubescence, which is deciduous as the fruits develop. The flowers of *C. panurensis* appear to be distylous, with the stamens partially exserted in the long-styled form and well exserted in the short-styled form; the floral biology of *C. tillettii* is unknown, but the flower described in its protologue resembles the short-styled form of distylous species. The corollas are described by collectors as white or cream and the fruits as maroon, dark purple, or dark red.

Carapichea panurensis appears not to have been treated taxonomically since it was described, when

Mueller (1881) classified it in *Mapouria* and included it in a group with several other species that are included here in *Carapichea* or have been transferred to *Margaritopsis* (Taylor, 2005). Steyermark included *C. tillettii* in *Psychotria* sect. *Chytropsia* (Bremek.) Steyerm. (1972: 484, 496; as *P. tillettii*), which comprised a heterogeneous group of species; several of those are now included in *Margaritopsis* (Taylor, 2005) and others appear to belong to *Rudgea* (Taylor et al., in prep.). The two species of the *Panurensis* group both have the characteristic stipule morphology of *Carapichea*.

19. Carapichea panurensis (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Mapouria panurensis* Müll. Arg., Flora 59: 460. 1876. *Uragoga magnusiana* Kuntze, Revis. Gen. Pl. 2: 956. 1891, non *Uragoga panurensis* (Müll. Arg.) Kuntze, 1891. TYPE: Brazil. Amazonas: prope Panuré ad Rio Uaupes, Oct. 1852–Jan. 1853, *R. Spruce 2689* (holotype, BR!; isotypes, C not seen, C as photo F neg. #22841 at MO!, G!, P!).

This species is known from scrub forest, seasonal forest, or caatinga at elevations of ca. 100–150 m in northern Amazonian Brazil and adjacent southeastern Colombia. The stipules are well developed, and the leaves are relatively small and stiff in comparison to other species of *Carapichea* as well as generally obtuse at the apex, an unusual condition in this genus.

20. Carapichea tillettii (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria tillettii* Steyerm., Mem. New York Bot. Gard. 23: 496, fig. 70. 1972. TYPE: Guyana. Upper Mazaruni River Basin, in low forest near former village of Suru-a-gu-puh, at head of Suru-a-gu-puh River, 470 m, 12 Sep. 1960, *S. S. Tillett & C. L. Tillett 43946* (holotype, NY[00132844], NY digital image!).

This species is known from escarpment forest at elevations of 1070–1570 m in the highlands of Guyana. The protologue described this species as having opposite leaves but the leaf arrangement actually varies, with plants from Merume Mountain having opposite leaves, those from Mt. Wokomong having verticillate leaves, and plants from Mt. Ayanganna variable in this regard with one specimen from this last area (*D. Clarke et al. 9062*, MO) having both conditions on one stem.

VI. *Stachyococcus* Group

This group comprises two species found in lowland wet vegetation at elevations of 100–300 m in the western Amazon basin. These species share a green drying color, relatively small stipules, inflorescences with reduced bracts and the flowers arranged in dense glomerules or heads, and relatively large fruits. The leaves lack acarodomatia. The leaves of *Carapichea adinantha* have well-developed secondary veins and also several short intersecondary veins between each pair of secondary veins, and the higher-order venation is sometimes visible or sometimes not visible; the leaves of *C. verrucosa* have the secondary veins hardly visible and the remaining venation not visible. The corollas of *C. adinantha* are white with well-developed adaxial projections on the lobes, and the anthers and stigmas are both included and situated in the lower part of the corolla tube; its floral biology is unknown, but if these flowers are distylous they have an unusual arrangement. The flowers of *C. verrucosa* are unknown. The fruits of these two species are reported to be spongy and variously blue, violet, purple, yellow, brownish yellow, or white. The pyrenes of both species are relatively large and thin-walled; those of *C. verrucosa* are abaxially verrucose, a unique feature within the genus and perhaps in the Neotropical Psychotrieae and Palicoureeae.

21. Carapichea adinantha (Standl.) C. M. Taylor, comb. nov. Basionym: *Retiniphyllum adinanthum* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(5): 355. 1931. *Stachyococcus adinanthus* (Standl.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 13(6): 144. 1936. TYPE: Peru. Loreto: in clearing, Mishuyacu, near Iquitos, 100 m, Feb.–Mar. 1930, *G. Klug 988* (holotype, F-612612!; isotypes, NY[00133128], NY digital image!, US-1455972, US digital image!).

This species is known from wet forests on terra firme at elevations of ca. 100–200 m in Amazonian Peru, Colombia, and western Brazil. A description was presented by Taylor (1997: 636; as *Stachyococcus adinanthus*). This species is unusual in its spiciform inflorescences, corollas that are granular-puberulous on the external surfaces, and relatively large fruits with smooth, thin-walled pyrenes. The fruits are usually described as blue, violet, or purple, but one collector reported them to be white (*R. Vásquez & Soto 11870*, MO!) and another as black (*R. Vásquez & N. Jaramillo 10125*, MO!).

22. Carapichea verrucosa C. M. Taylor, sp. nov. TYPE: Peru. Loreto: prov. Maynas, distr. Punchana, Río Momón, trocha del caserio de San Antonio, en terreno alto, monte abierto y arcilloso, c. 120 m, 23 July 1998, *M. Rimachi Y.*

12346 (holotype, USM-185437!; isotype, MO-04904145!). Figure 2.

Haec species a congeneris inflorescentia capitata bracteis parvis, fructu satis grandi spongioso verrucoso albo usque brunneolo-flavido atque pyrenis abaxialiter verruculosis distinguitur.

Shrubs or trees, flowering at 1.5 m tall, to 8 m tall, somewhat fleshy, drying green to brown; stems subterete to subquadrate, glabrous. Leaves opposite; blades elliptic to elliptic-oblong, 10–26 × 2.6–9.8 cm, drying chartaceous, glabrous on both surfaces, at base acute to cuneate, at apex acuminate with tips 0.8–2.5 cm and often curved; secondary veins 5 to 8 pairs, usually looping to interconnect at least in basal part of blade, weakly visible, remaining venation not visible, adaxially with midrib plane to thinly prominulous and remaining venation plane, abaxially with midrib thinly prominent, secondary veins prominulous to plane, and remaining venation plane; petioles 10–27 mm; stipules interpetiolar, narrowly triangular to lanceolate or ligulate, 6–15 × 3–6 mm, obtuse to acute or sometimes weakly erose, glabrous, becoming dry, brown, and stiffly papery to somewhat indurated from apex downward, fragmenting with age, usually leaving an irregular, persistent basal portion. Inflorescences terminal, capitate to subcapitate or shortly spiciform; peduncle 0.8–2 cm, puberulous, flattened; heads (not including fruits) 1–2 × 1–1.2 cm, 15- to 30-flowered; bracts broadly triangular to rounded, 0.8–1.2 mm, glabrous, subtending several outermost flowers of groups. Flowers (postanthesis) sessile or subsessile; ovary portion obconic, ca. 1 mm, glabrous; calyx limb 1–1.2 mm, truncate to sinuate or shallowly, irregularly lobed, glabrous; corolla, anthers, and stigmas not seen. Fruits ellipsoid, yellow, brownish yellow, or creamy white, 2.5–3 × 2–2.5 mm, spongy, with thickened ring at apex, covered with low warty or scabrous growths or points; pyrenes 2, planoconvex, bony, abaxially smooth except weakly verrucose, adaxially smooth with raphal plug and thin median furrow that connects at apex to 2 marginal furrows, dehiscent through raphal plug and adaxial furrow.

Habitat, distribution, and phenology. This species is known from wet, noninundated forests at elevations of 100–300 m in the northwestern Amazonian basin of Brazil, Colombia, and Peru; it has been collected with fruits in April, June, July, and November.

IUCN Red List category. *Carapichea verrucosa* does not meet the geographic range criteria for any threatened category in its extent of occurrence (EOO) but meets the criterion for Endangered in its limited AOO based on the widely scattered collection localities. This species is known from six localities (i.e., different threat regimes) and is found in two different legally protected areas in two countries across a linear geographic range of 1200 km. It is apparently not common locally, but it is widespread. It is here assessed as Least Concern (LC).

Notes. This new species is notable for its relatively large, spongy, creamy white, yellow, or yellowish brown fruits with a finely warty exterior and a thickened ring at the apex and for its pyrenes that are verruculose on the abaxial surface; the specific epithet refers to the warty surfaces of the fruits and pyrenes.

Paratypes. BRAZIL. **Acre:** Sena Madureira, Faz. São Jorge I, BR-364 Km. 107, ramal de Toco Preto, 9°26′S, 68°37′W, *H. Medeiros, C. C. Berg, W. Castro, E. C. Oliveira, F. A. Obermuller & M. Silveira 476* (MO). COLOMBIA. **Amazonas:** correg. Araracuara, Parcela No. 16, 0°56′S, 71°47′W, *A. Duque, A. M. Benavides, A. León, A. Matapi "y otros" 8061* (COAH); mpio. Leticia, correg. Tarapacá, Parque Nac. Nat. Amacayacu, Cabaña Loreno (Río Cotuhé), *A. Rudas, P. Palacios, S. Duque, F. del Aguilar Joaquín & G. Morán 2427* (COL, MO). PERU. **Loreto:** prov. Loreto, Nauta, Río Marañón, *R. Vásquez & N. Jaramillo 3431* (AMAZ, MO, USM). **Ucayali:** E of Aguaytia, betw. Pucallpa Rd. & Río Aguaytia, *M. E. Mathias & D. Taylor 5015* (MO, USM).

VII. Bahia Group

This group comprises one species found in lowland Atlantic forests in eastern Brazil. This species is unusual in *Carapichea* for its deeply bilobed stipules with very narrow lobes, but the stipules are similar to those of other species in this genus in becoming marcescent and then fragmenting and falling off before the leaves, and some other species of *Carapichea* also have bilobed stipules (e.g., *C. guianensis*, *C. tillettii*). The leaves lack acarodomatia, and have few visible intersecondary veins with the higher-order venation usually not visible. The floral biology of this species is unknown, but the flowers described in the protologue are similar to the short-styled form of distylous species. The fruits are described as deep purple.

23. Carapichea lucida J. G. Jardim & Zappi, Kew Bull. 63(4): 661, fig. 1. 2008. TYPE: Brazil. Bahia: Elísio Medrado, ca. 1 km Monte Cruzeiro, Reserva Particular Jequitibá, Serra da Jibóia, 12°52′S, 39°28′W, 600–650 m, 1 Dec. 2004, *J.[G.] Jardim et al. 4280* (holotype, HUEFS not seen; isotype, CEPEC not seen).

This species is found in Atlantic forests at elevations of 200–800 m in Bahia State in eastern

Brazil. It is distinctive in *Carapichea* for the combination of its stipules with two well-developed narrow lobes and its capitate inflorescences with large, shiny, bright green bracts. A description and illustration were presented by Jardim and Zappi (2008). This is the only species of *Carapichea* so far known from eastern Brazil. The additional collectors of the type specimen are not listed in the protologue.

Excluded Name

Carapichea patrisii DC., Prodr. 4: 536. 1830. *Cephaelis patrisii* (DC.) D. Dietr., Syn. Pl. 1: 773. 1839. *Uragoga carapichea* Kuntze, Revis. Gen. Pl. 2: 955. 1891, non *Uragoga patrisii* (DC.) Kuntze, 1891. TYPE: French Guiana. S. loc., *Patris s.n.* (holotype, G-DC not seen; isotype, G!). [= *Psychotria hoffmannseggiana* (Willd. ex Roem. & Schult.) Müll. Arg. (Steyermark, 1972)].

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Appendix 1. Alphabetical List of Accepted Species

The number following a plant name indicates the order of treatment in this article. Additional information including synonymy can be found in this article and also in the TROPICOS online database.

Carapichea adinantha (Standl.) C. M. Taylor, 21
C. affinis (Standl.) L. Andersson, 2
C. altsonii (Sandwith) C. M. Taylor, 15
C. araguariensis (Steyerm.) C. M. Taylor, 9
C. crebrinervia (Standl.) C. M. Taylor, 10
C. dolichophylla (Standl.) C. M. Taylor, 3
C. fimbriflora (Steyerm.) C. M. Taylor, 11
C. franquevilleana (Müll. Arg.) C. M. Taylor, 4
C. guianensis Aubl., 5
C. ipecacuanha (Brot.) L. Andersson, 1
C. klugii (Standl.) C. M. Taylor, 6
C. ligularis (Rudge) Delprete, 12
C. lucida J. G. Jardim & Zappi, 23
C. maturacensis (Steyerm.) C. M. Taylor, 7
C. necopinata (Standl.) C. M. Taylor, 13
C. nivea (Sandwith) C. M. Taylor, 16
C. pacimonica (Müll. Arg.) C. M. Taylor, 14
C. panurensis (Müll. Arg.) C. M. Taylor, 19
C. sandwithiana (Steyerm.) C. M. Taylor, 17
C. tillettii (Steyerm.) C. M. Taylor, 20
C. urniformis (Steyerm.) C. M. Taylor, 18
C. vasivensis (Müll. Arg.) C. M. Taylor, 8
C. verrucosa C. M. Taylor, 22